DESCRIPTIONS *of* NEW SHARKS AND RAYS *from* BORNEO

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Foreword

This sequence of taxonomic papers is the consequence of two major surveys of the chondrichthyan fauna of Borneo. In 1996, the first major investigation of the sharks and rays of Sabah was initiated through funding from the UK Darwin Foundation. This project addressed questions relating to the biodiversity, fisheries impact, biology, and conservation status of the coastal marine and freshwater elasmobranch fauna, and resulted in the compilation of the first checklist of chondrichthyans of greater Borneo. The Darwin survey also provided the impetus for a larger survey in the last decade of fish markets of the island, incorporating both Malaysian Borneo and Indonesian Borneo. This comprehensive survey, made possible by the financial support of the National Science Foundation (grants NSF BS&I Nos. DEB 0103640, DEB 0542941, DEB 0542846), and parallel surveys of the chondrichthyan faunas of the Philippines and eastern Indonesia, unearthed several taxonomic problems that needed resolving, particularly involving cryptic speciation and nomenclature.

The main objective of this special taxonomic publication is to document updated names for some of the species that were once considered widespread in the Indo-Pacific, but which are now known to have more restricted distributions. Seven new species are formally described, three species are resurrected, and two other poorly known species are redescribed in 11 separate papers. These names will be used in the soon to be published guide to the chondrichthyans of Borneo, 'Sharks and rays of Borneo' (in press). Morphometric acronyms used in tables follow Compagno (1984, see Appendix 1).

Research for these papers extends over two decades and has involved many people in many different ways. On behalf on the authors of these papers, the editors wish to thanks the following for their help:

Gaining access to material in ichthyological collections was vital to this study. We thank the staff at these facilities: Renny Kurnia Hadiaty and Ahmad Jauhar Arief (Museum Zoologicum Bogoriense, MZB); Albert Lo and George Jonis (Sabah Museum, SMEC); Dave Catania (California Academy of Sciences, CAS); Morice Rowan, Stefanus Simon and Syuhaime Ahmat Ali (Borneo Marine Research Institute, BRMI); Martien van Oijen and Ronald de Ruiter (Rijksmuseum van Natuurlijke Histoire, RMNH); Romain Causse, Bernard Séret, Guy Duhamel, Patrice Pruvost and Zora Gabsi (Muséum national d'Histoire naturelle, MNHN); Patrick Campbell and Oliver Crimmen (British Museum of Natural History, BMNH); Peter Bartsch (Museum fur Naturkunde, ZMB); Ronald Vonk and Hielke Praagman (Zoologisch Museum, ZMA); Gento Shinohara (National Science Museum, NSMT); Toshio Kawai (Hokkaido University, HUMZ); Masato Moteki (Tokyo University Marine Science, MTUF); Jeffrey Williams and Jerry Finan (Smithsonian Institution National Museum of Natural History, USNM); Richard Feeney (Los Angeles County Museum, LACM); Hiroyuki Motomura (Kagoshima University Museum, KAUM); Simon Weigmann (Zoologisches Institut und Zoologisches Museum der Humboldt Universität, ZMH); Kelvin Lim (National University of Singapore, NUS); Ernst Mikschi (Naturhistorisches Museum, Vienna, NMW); Mohammed Adrim, Indra Aswandi, Priyo Agustono, Suharsono (Director of Research Centre for Oceanography LIPI, Jakarta); Mark McGrouther and Amanda Hay (Australian Museum, AMS); Helen Larson, Gavin Dally and Barry Russell (Northern Territory Museum, NTM); Sue Morrison, Glen Moore and Barry Hutchins (Western Australian Museum, WAM); Jeff Johnson (Queensland Museum, QM). Chondrichthyan specialists, Bernard Séret, Charlie Huveneers, Jenny Kemper, Dave Ebert, Peter Kyne and Ken Graham, also provided reviews of papers submitted.

Several people helped in securing collecting permits, and collecting or providing access to specimens from Borneo and nearby regions. In particular these include: Albert Chuan Gambang (Fisheries Research Institute Sarawak); Ridzwan Abdul Rahman (Borneo Marine Research Institute); Edward Rooney Biusing (former Deputy Director Fisheries Sabah); Ono Kurnaen Sumadhinarga, Dedy Darnaedi, Ruben Silitonga and Sri Wahyono (LIPI); Hilconida Calumpong, Clarissa Reboton and May Luchavez-Maypa (Silliman University, Philippines); and several other local and international scientists and volunteers, including Sarah Fowler, Scott Mycock, Sid Cook, Michael Sugden, Andy Oliver, Annadel Cabanban, Loren Caira, Claire Healy, George Chong, Hamri bin Hgi-Kating, Latip Sait, Asni Etin, Masni Etin, Salik Etin, Anchain, Roslie, Justin Tampuling, Mengke, Junardi, Mugi Utomo, Zainal Abidin, Rayner Galid, Charles Greenwald, Isnol Alang, Joe Guadiano, Badi Samaniego and Dharmadi.

The genetics component of this research provided important insights and we sought the help of several colleagues, particularly Kerri Matthes, Clemens Lakner and Neil Aschliman (Florida State University), Dirk Steinke and Paul Hebert (University of Guelph), Bob Ward, Melody Puckridge and Bronwyn Holmes (CSIRO), and Shannon Corrigan (Macquarie University).

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We particularly thank all the authors and reviewers of papers in this volume for their assistance in completing this work within a short timeframe.

Peter R. Last
William T. White
John J. Pogonoski

Contents

A new wobbegong shark, *Orectolobus leptolineatus* sp. nov. (Orectolobiformes: Orectolobidae), from the Western Central Pacific

Peter R. Last, John J. Pogonoski & William T. White

CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA

ABSTRACT.— A new *Orectolobus* species, collected from the Indo-Malay Archipelago and western North Pacific, is described and figured from specimens collected in eastern Indonesia. *Orectolobus leptolineatus* sp. nov., a medium-sized wobbegong reaching about 120 cm TL, is characterised by a striking colour pattern of fine vermiculations, bands, saddles and ocelli. It has been confused with a very similar congener, *O. japonicus*, from which it differs mainly in morphometrics and coloration, found in the Japanese Archipelago. Species previously referred to as *Orectolobus japonicus* likely form a complex of very closely related western Pacific species that require further morphological and molecular examination to elucidate their taxonomic complexity.

Key words: *Orectolobus leptolineatus* – new species – Orectolobiformes – wobbegong shark – Western Central Pacific

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

Wobbegong sharks (F. Orectolobidae) are represented in the Indo–Pacific by three genera and 11 valid nominal species (Last *et al*., 2008; Corrigan & Beheregaray, 2009): *Eucrossorhinus dasypogon* (Bleeker, 1867); *Orectolobus floridus* Last & Chidlow, 2008; *O. halei* Whitley, 1940; *O. hutchinsi* Last, Chidlow & Compagno, 2006; *O. japonicus* Regan, 1906; *O. maculatus* (Bonnaterre, 1788); *O. ornatus* (De Vis, 1883), *O. parvimaculatus* Last & Chidlow, 2008; *O. reticulatus* Last, Pogonoski & White, 2008; *O. wardi* Whitley, 1939; and *Sutorectus tentaculatus* (Peters, 1864). Of these, only *O. japonicus*, which is widely considered to be widespread in the western North Pacific, is not known from Australian waters (Last & Stevens, 2009).

Goto (2008) revised the genus *Orectolobus* in Japan, concluding that a single species, *O. japonicus* from the western North Pacific, was valid. He noted that references to *O. maculatus* and *O. ornatus* in the Japanese literature were erroneous identifications of *O. japonicus*. Goto examined specimens from the main islands of Japan as well as the Okinawa region to the south, but specimens from these two regions comprise two forms that differ in both colour pattern and morphometrics. Subtle morphological variations may have been masked in his paper by combining the data for more than one species. In addition, although he separated the data of males from females, Goto combined the data of juveniles and adults. Last & Chidlow (2008) demonstrated that wobbegongs can display significant ontogenetic differences, which can lead to large ranges for morphometric features (e.g. dorsal-fin height) that can be missed if sizes of individuals are not taken into account.

Shen (1993) figured two species of *Orectolobus* from Taiwan, and although both identifications are now incorrect, the presence of two forms in Taiwan is confirmed; assuming the locality information for his images is correct.

In 1996, the skin of an unidentifiable wobbegong with a strikingly reticulate colour pattern was collected during a survey of the elasmobranchs of Borneo, funded by the British Darwin Foundation (Manjaji, 2002). More recently, complete specimens of similar colour forms have been collected from the nearby Philippines (as *O.* cf. *ornatus*: Compagno *et al.*, 2005), Indonesia (as *O.* cf. *ornatus*: White *et al*., 2006; Corrigan & Beheregaray, 2009), Borneo (as *O. maculatus*: Yano *et al*., 2005), and Taiwan (AMS I 43794–002). Based on genetic studies (as *O.* cf. *ornatus*: Corrigan & Beheregaray, 2009), the new species is distinct from *O. ornatus* and *O. maculatus*, which are only confirmed from Australian waters. The new species is described and figured below and compared to its closest congeners.

METHODS

Terminology for external structures and methodology for measurements follows the widely used scheme proposed by Compagno (1984) with some modifications initiated by Last *et al*., 2006. Measurements were direct (taken from point to point) unless otherwise specified. The prenarial length (PRN) was taken almost transversely from the middle of the snout tip to the junction of the nostril and nasal barbel; intereye (INE) taken rather than interorbital distance (INO); mouth width (MOW) taken as the width across the jaws to their outer lateral angles; ventral caudal margin was not subdivided into highly subjective measurements of the preventral caudal (CPV) and lower postventral (CPL) margins; and preorbital and spiracular lengths were taken from the clearly defined anterior edges of the eye and spiracle respectively. Measurements and counts were made for the dermal lobe configurations consisting of two groups of preorbital lobes and two postspiracular lobes (Last *et al*., 2006): the first preorbital group (PO1) extends from near the posterolateral margin of the nostril to the end of the first distinct grouping on the snout above the upper jaw; the second preorbital group (PO2) extends from just forward of the eye (or near the jaw angle) to below the eye (difficult to determine the junction between these groups in some species); the first postspiracular group (PS1) consists of a single small lobe below the hind margin of the spiracle; the second postspiracular group (PS2) is closer to the gill slits than the spiracle, and is often rudimentary or simple. Measurements were taken sequentially between points A–F (see Fig. 1 in Last *et al*., 2006) where A is the origin of the nasal barbel; B the insertion of PO2; C, D the respective origin and insertion of PS1; and E, F the respective origin and insertion of PS2.

A comprehensive series of measurements were taken for the holotype (MZB 18623) and 5 of the paratypes (CSIRO H 5787–01, CSIRO H 5787–02, CSIRO H 5876–03, CSIRO H 6128–06, CSIRO H 6138–02) of the new species and converted to percentages of total length (Table 1). In the description, morphometric data for the holotype are provided followed by ranges for the 5 measured paratypes in parentheses. Additional ratios of selected measurements are included in the species description. Morphometrics on Japanese specimens (HUMZ & BMNH) were taken during the senior author's visit to those institutions in 2001 and 2009 respectively; morphometrics on specimens in the CSIRO Australian National Fish Collection were taken by JP in 2009–2010 after strict confirmation of methodology with the senior author. Not all measurements were taken on the HUMZ specimens; these are excluded from Table 1. Counts of monospondylous, diplospondylous, and total centra were obtained from radiographs for the holotype (MZB 18623) and 7 paratypes (CSIRO H 5787–01, CSIRO H 5787–02, CSIRO H 5876–03, CSIRO H 6128–06, CSIRO H 6138–02 and H 6446–03, 2 embryos). Dermal lobe counts were taken for the above specimens plus an additional paratype, Indo-Oz L 154. Tooth row counts, which were taken directly from specimens, were confirmed by dissection from a paratype (CSIRO H 5787–01). Dentition terminology is based on Compagno (1970, 1979, 1988). Vertebral count terminology follows Compagno (1979, 1988); precaudal vertebral counts were taken to the dorsal-caudal origin; all counts of the new species were taken by the one reader (JJP) to ensure consistency. The distal vertebrae of the caudal fin in orectolobids are often faint or blurred on radiographs, so accuracy for total vertebral counts is predicted as +/– 1–2 vertebrae. A spiral valve count was performed on one paratype (CSIRO H 5787–01) by removing the valve and dissecting it lengthwise to allow full view of the intestinal turns. Two of the authors independently counted the spiral valves and recorded the same value.

Abbreviations for field, accession, and catalogue numbers follow Leviton *et al*. (1985): AMS – Australian Museum, Sydney; BMNH – British Museum of Natural History, London; CSIRO – Australian National Fish Collection, Hobart; HUMZ – Hokkaido University Laboratory of Marine Zoology, Faculty of Fisheries, The Hokkaido University Museum, Hakodate, Hokkaido, Japan; MZB – Museum Zoologicum Bogoriense, Jakarta; SMBL – Kyoto University, Seto Marine Biology Laboratory, Wakayama Prefecture, Japan; Indo–Oz – Indonesian Elasmobranch Project field accession numbers (specimen to be deposited into either CSIRO or MZB collections in the future).

Orectolobus leptolineatus sp. nov.

Figs 1–3, 4a, 5a,b, 6; Table 1

?*Orectolobus japonicus* (non Regan, 1906): Shen, 1993, 613, pl. 3.10 (Taiwan?).
?*Orectolobus* cf. *ornatus* (De Vis, 1883): Compagno *et al*., 2005, 20, 103, fig 1c (Cebu, Philippines).
Orectolobus cf. *ornatus* (De Vis, 1883): White *et al*., 2006, 88–89 (Indonesia); Corrigan & Beheregaray, 2009, 207–209, 212, figs 2–3.
Orectolobus maculatus (non Bonnaterre, 1788): Pickell & Siagian, 2000, 114–115, 120 (Bali, Indonesia); Yano *et al*., 2005 (in part, Sarawak figure), 82–84, pl. 47.

Holotype. MZB 18623, adult male 887 mm TL, Kedonganan fish market, Bali, Indonesia, ca. 08º45′ S, 115º01′ E, 27 Apr. 2004.
Paratypes. 11 specimens: CSIRO H 5787–01, adult male 1000 mm TL, CSIRO H 5787–02, adult male 920 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 08 Jul. 2001; CSIRO H 5876–03, female 992 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 06 Jun. 2002; CSIRO H 6128–06, female 849 mm TL, Kedonganan fish market, south-west coast of Bali, Indonesia, ca. 08º45′ S, 115º01′ E, 12 Oct. 2002; CSIRO H 6138–02, adult male 930 mm TL, MZB

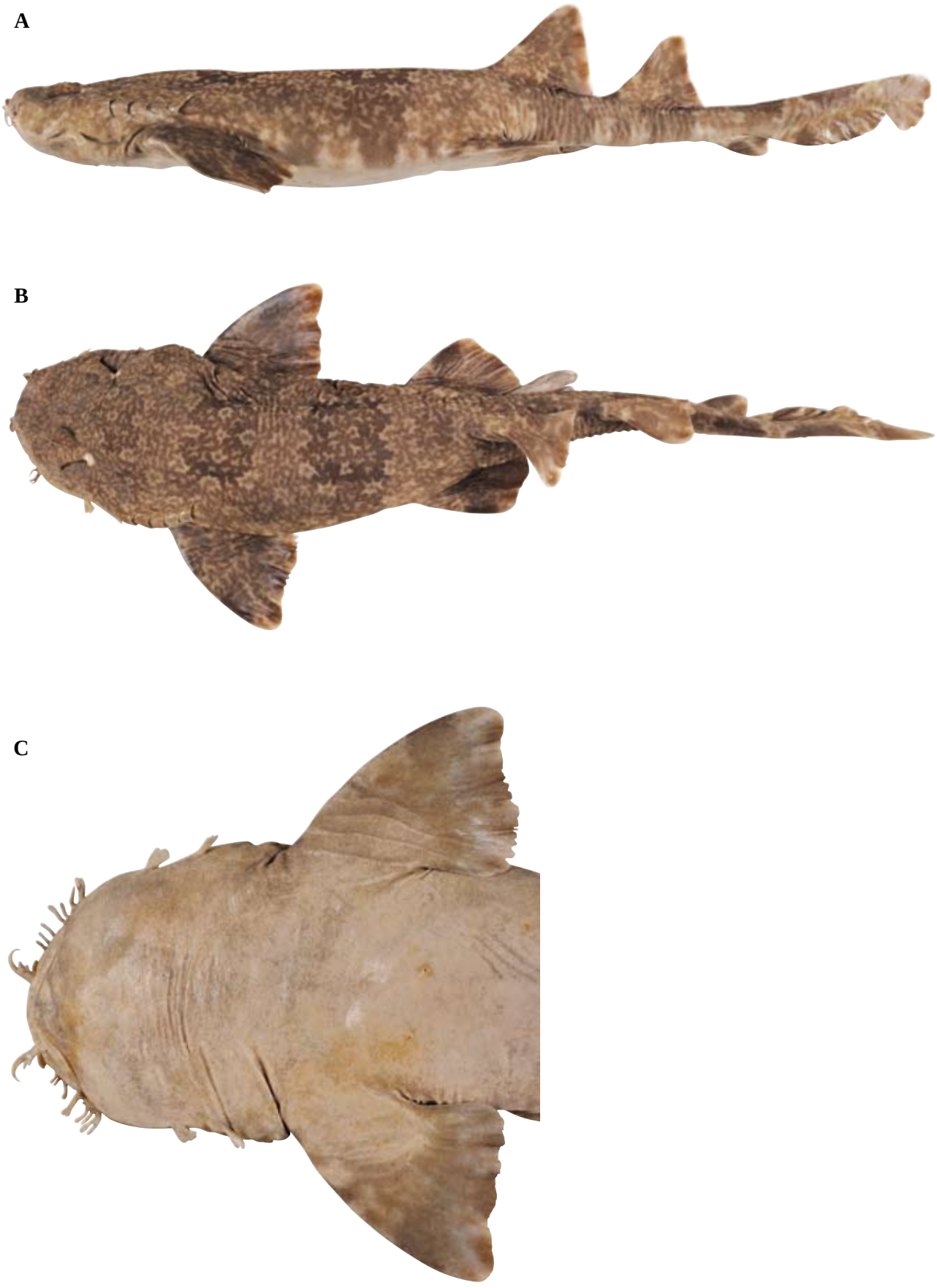

Figure 1. *Orectolobus leptolineatus* sp. nov., adult male holotype (MZB 18623, 887 mm TL, preserved): A. lateral view; B. dorsal view; C. ventral view of head.

15471, adult male 950 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 25 Mar. 2002; CSIRO H 6446–03, 2 mid-term female embryos 131–140 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 18 Aug. 2005; MZB 15100, female 940 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 08 Jun. 2002; MZB 15435, female ca. 780 mm TL, Tanjung Luar fish market, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 11 Oct. 2004; Indo–Oz L154, female 436 mm TL, south-east coast of Lombok, Indonesia, ca. 08º45′ S, 116º35′ E, 28 Mar. 2006.

DIAGNOSIS.— A medium-sized *Orectolobus* (to at least 120 cm TL) with the following combination of characters: coloration complex and variable, strongly vermiculate over dorsal and lateral surfaces with alternating dark brownish bars and saddles; dorsal and upper surface of paired fins with prominent vermicular patterns; ventral surface of trunk mainly uniformly pale; nasal barbel with a branch; preorbital dermal lobes complex, with 2–3 simple lobes in PO1 group and 3–4 simple to terminally branched lobes in PO2; postspiracular dermal lobes simple, well developed, thallate, distance across preorbital group 1.3–1.6 times interspace between preorbital group and postspiracular lobe (PO/PO–PS1), 6.5–8.0 times base length of anterior postspiracular lobe (PO/PS1); base of anterior postspiracular lobe 4.3–5.3 in its distance from postorbital group (PO–PS1/PS1), 2.5–2.9 in its distance from posterior postspiracular lobe (PS1–PS2/PS1); no enlarged supraocular knob or warty tubercles on back; dorsal fins tall, upright; first dorsal-fin origin near insertion of pelvic fin; tip of pelvic fin below insertion of first dorsal fin; interdorsal space 0.5–0.8 times anal-fin base length; anal-fin inner margin 0.7–0.8 of anal-fin posterior margin; tooth rows in upper jaw 23 (n=1), rudimentary row of teeth at symphysis of upper jaw usually present; monospondylous centra 44–51; total vertebral centra about 148–163.

DESCRIPTION.— Body firm, robust; trunk slightly depressed; deepest over mid-trunk; not tapering abruptly at pelvic-fin insertion, tail subcircular in cross-section, slightly compressed near base of caudal fin. Head broad, somewhat oval in cross-section, truncate to slightly convex anteriorly when viewed from above; moderately depressed, height at eye 7.4% in holotype (6.2–8.5% in paratypes) TL; abdomen moderately elongate, pectoral–pelvic space 18.4 (14.7–19.8)% TL, 0.81 (0.61–0.83) of head length; pelvic–anal space 3.91 (2.43–3.12) times anal-fin base; caudal peduncle rudimentary, caudal fin almost connected to anal-fin insertion, compressed slightly, narrowly oval in cross section at anal-caudal junction, height 0.97 (0.91–1.23) times width at second dorsal-fin insertion, 1.37 (1.05–1.30) times width at anal-fin insertion.

Snout short, bluntly rounded in lateral view, almost truncate to broadly convex in dorsoventral view; slightly expanded above nostrils dorsally; preorbital pit usually obscure; snout symphysis weakly indented anteriorly (variable in paratypes); preoral length 1.0 (1.0–1.4)% TL, 11.1 (8.3–11.6) in mouth width; prenarial snout 1.37 (1.24–1.45) times eye length. Eyes dorsal on head, small, slit-like, length 2.0 (1.8–2.2)% TL, 11.32 (10.75–13.52) in head length, supraorbital crest elevated slightly over and behind eye, supraocular knob weak to absent; subocular pocket moderately well-developed, almost straight (curved in some paratypes), its length slightly longer than eye; interorbit almost flat, inter-eye distance 3.47 (3.25–3.95) times eye length, 1.02 (1.01–1.21) times direct preorbital length, 0.75 (0.70–0.79) times direct prespiracular length, 2.12 (2.09–2.40) times spiracle length. Spiracle large, slit-like, oblique to horizontal axis, much longer than eye length; anterior margin concave, well elevated above flattened posterior margin (sometimes appearing as a raised fleshy ridge); posterior margin almost flat to forming a slight depression leading into spiracle. Gill slits slightly dorsolateral on head; 2nd over origin of pectoral fin, 3rd to 5th above pectoral-fin base; last gill slit longest, 1.34 (1.17–1.31) times 4th, located over anterior third of midbase of pectoral fin; first 4 more or less equally spaced, 4th and 5th usually closer together; upper edge of slits becoming increasingly more dorsal from 1st to 5th.

Mouth large, horizontally expanded, broadly arched, lower jaw slightly inferior, width 11.0 (10.9–11.6)% TL, 1.40 (1.37–1.51) in head width at eye; upper labial furrows originating at nostrils; lower labial furrows longer, almost connected at symphysis of lower jaw, length 0.52 (0.45–0.56) of mouth width; symphysial groove very deep, well developed, its length exceeding distance between lower labial furrows. Teeth unicuspid, pointed, widely spaced, central cusps not flanked by small lateral cusps (non-type with inconspicuous lateral cusps in the distal region); largest near symphysis, 2 rows of enlarged canines in upper jaw, 3 rows in lower jaw; teeth adjacent to enlarged canines about half length of those in upper jaw, more than half length of those in lower jaw; 23 rows in upper jaw, 17 in lower jaw (in paratype CSIRO H 5787–01); very small near jaw angle, sometimes weakly cuspid; outer anterior pair of teeth of upper jaw barely exposed when mouth closed; rudimentary symphysial canines in upper jaw (sometimes present in paratypes).

Nostrils small, widely separated, internarial space 5.4 (5.0–5.3)% TL; adjacent upper lip of mouth; posterior lobe well developed, forming an expanded, broad tube-like flap. Nasal barbel subterminal on head, digitiform, its base flattened, but becoming more rounded and tapering distally; with an enlarged, broad-based, flattened, shallowly bifurcate (usually weakly thallate or single lobed in paratypes) anterolaterally directed lobe near its midlength; barbel length slightly shorter than upper labial furrow, 3.8 (3.5–4.2)% TL. Dermal lobe band well developed; PO1 with 3 (2–3), slender, slightly flattened,

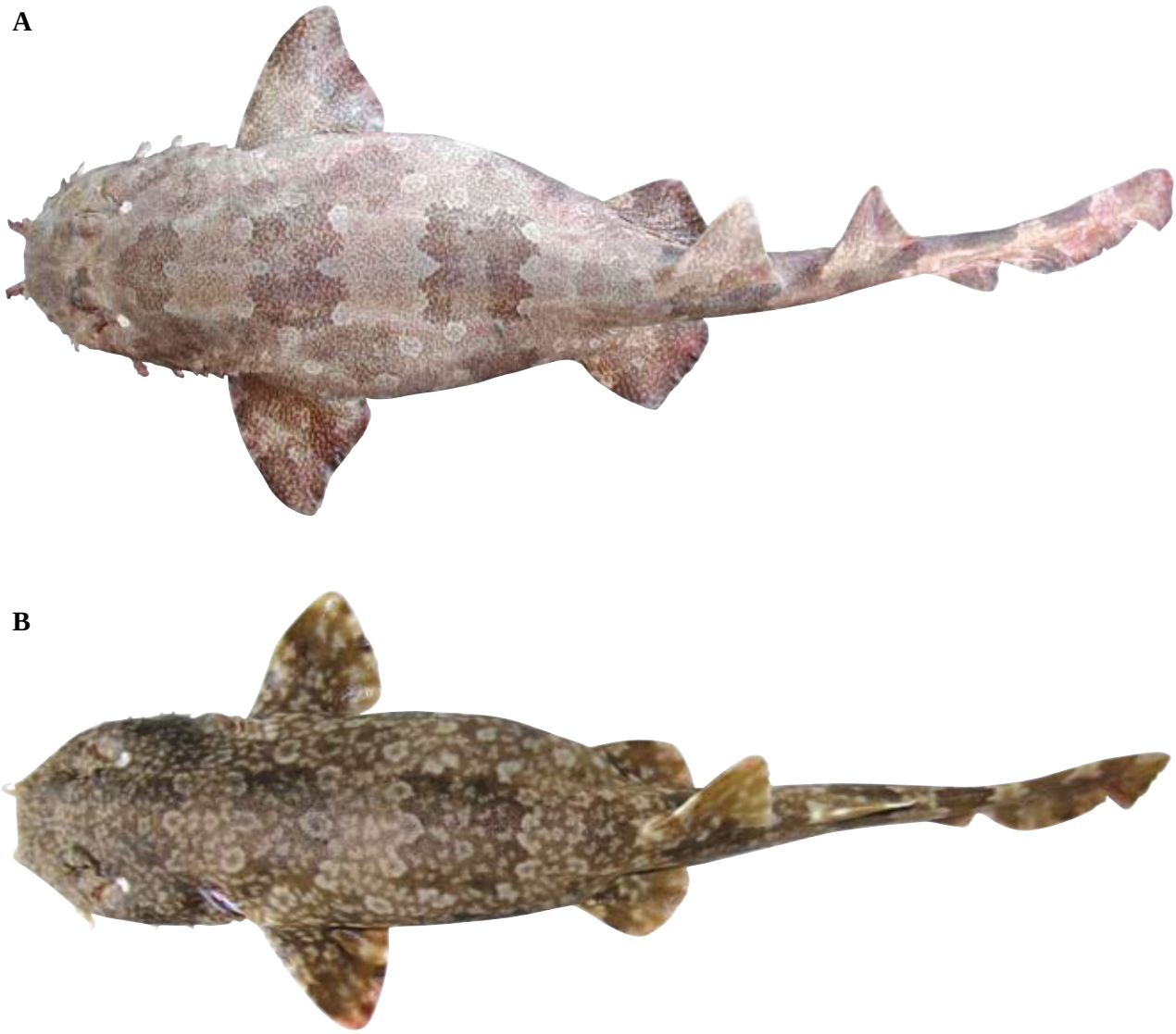

Figure 2. Dorsal view of *Orectolobus leptolineatus* sp. nov.: A. female paratype (CSIRO H 5876–03, 992 mm TL, fresh); B. female paratype (Indo–Oz L154, 436 mm TL, fresh).

simple lobes, last usually longest; PO2 origin near jaw angle, with 4 (3–4) longer-based, more flattened, simple to complex lobes, usually branched distally into two extremities in either the first, last or both; PS1 very broadly thallate with shallowly incised outer margin (varying in paratypes from simple to irregular), base usually preceded by short, ridge-like, but well-developed lateral skin fold; PS2 variable, simple to shallowly incised, thallate, slightly smaller than PS1 (in paratypes subequal to smaller); PO distance 1.34 (1.47–1.58) times PO–PS1 interspace; PO distance 6.98 (6.49–8.04) times PS1 base length; PO–PS1 interspace 5.21 (4.29–5.34) times PS1 base length; PS1–PS2 interspace 2.76 (2.50–2.86) times PS1 base length.

Dermal denticles (adult male holotype) on flank minute, unicuspidate, tightly packed and weakly imbricate; skin velvety; pedicels short, strong; crowns small, mostly arrowhead-shaped, median ridge greatly elevated posteriorly, weak lateral ridges sometimes evident. On head, crowns very variable in shape (somewhat flatter in female paratype, CSIRO H 5876–03) with irregular margins; globular with crenulate anterior margins and bluntly angular posterior margins; median ridge usually elevated posteriorly to form a blunt knob. Denticles along lateral margin of spiracle with leaf-like crowns, sometimes with weak lateral cusplets; innermost denticles of spiracle slightly elongate, bristle-like. No crest of enlarged denticles at base of caudal fin or tubercles on dorsal surface of body. Clasper elongate, expanded

Table 1. Morphometric data for the holotype of *Orectolobus leptolineatus* sp. nov. (MZB 18623), with ranges and means provided for the measured paratypes, and for the syntype of *O. japonicus* (BMNH 1862.11.1.18), with ranges for two non-type specimens of *O. japonicus*.

	O. leptolineatus sp. nov.				*O. japonicus*		
	Paratypes (n = 5)				Non-types (n = 2)		
	Holotype	Min.	Max.	Mean	Syntype	Min	Max
TL–Total length (mm)	887	849	1000	938	753	538	1018
PRC–Precaudal length	77.9	77.2	81.7	78.9	78.2	77.7	78.4
PD1–Pre-first dorsal length	46.4	47.0	50.5	48.6	46.9	44.3	46.9
PD2–Pre-second dorsal length	60.1	61.7	63.4	62.3	61.8	58.7	60.7
PP1–Prepectoral length	19.9	20.7	22.2	21.5	19.8	17.4	18.1
PP2–Prepelvic length	43.5	40.9	44.4	43.0	43.6	41.0	41.9
SVL–Snout-vent length	46.2	46.5	50.1	47.9	46.5	43.6	46.1
PAL–Preanal length	72.7	70.4	73.6	71.7	70.5	–	–
IDS–Interdorsal space	4.9	4.2	5.0	4.7	4.8	3.8	4.4
DCS–Dorsal–caudal space	8.3	5.8	7.6	7.0	6.9	7.4	8.8
HDL–Head length	22.9	23.5	24.7	24.0	21.3	21.6	22.1
PG1–Prebranchial length	18.1	17.6	19.3	18.6	16.6	16.8	17.3
PSPd–Prespiracular length	9.3	9.3	10.0	9.8	8.6	8.5	9.2
POBd–Preorbital length	6.9	6.1	7.0	6.7	6.4	6.1	6.4
PRN–Prenarial length	2.8	2.6	2.9	2.7	–	–	–
POR–Preoral length	1.0	1.0	1.4	1.1	1.1	0.6	0.7
EYL–Eye length	2.0	1.8	2.2	2.1	1.9	1.6	1.7
EYH–Eye height	0.2	0.4	0.6	0.5	0.4	0.2	0.2
INE–Intereye space	7.0	7.0	7.5	7.3	6.8	6.7	6.9
SOD–Subocular pocket length	3.4	3.1	3.7	3.3	3.6	–	–
SPL–Spiracle length	3.3	3.0	3.4	3.2	3.1	2.9	3.2
ESL–Eye–spiracle space	2.0	1.8	2.2	2.0	1.7	1.6	1.7
NOW–Nostril width	0.7	0.7	0.9	0.8	1.1	1.1	1.2
INW–Internarial space	5.4	5.0	5.3	5.2	5.0	4.7	4.8
ANF–Anterior nasal flap length (barbel)	3.8	3.5	4.2	3.9	3.5	2.7	4.2
MOL–Mouth length	3.0	2.6	3.2	2.9	2.7	–	–
MOW–Mouth width (across jaws)	11.0	10.9	11.6	11.2	10.7	–	–
ULA–Upper labial furrow length	4.5	4.4	4.9	4.6	4.2	–	–
LLA–Lower labial furrow length	5.7	5.3	6.1	5.6	5.1	–	–
GS1–First gill-slit height	2.2	2.2	2.7	2.4	2.2	2.1	2.8
GS2–Second gill-slit height	2.6	2.4	2.7	2.5	2.1	–	–
GS3–Third gill-slit height	2.4	2.3	2.6	2.5	2.1	–	–
GS4–Fourth gill-slit height	2.1	2.1	2.5	2.3	2.2	–	–
GS5–Fifth gill-slit height	2.7	2.7	3.1	2.9	2.3	2.3	2.8
D1L–First dorsal-fin length	13.7	12.8	14.8	13.7	13.9	14.4	14.9
D1A–First dorsal-fin anterior margin	13.1	11.8	12.9	12.5	–	–	–
D1B–First dorsal-fin base	9.9	9.0	10.7	9.8	9.9	10.2	10.6
D1H–First dorsal-fin height	9.5	9.2	10.0	9.5	8.5	8.8	9.1
D1I–First dorsal-fin inner margin	4.2	4.0	4.5	4.3	4.6	4.2	4.9
D1P–First dorsal-fin posterior margin	9.8	9.2	10.9	9.9	8.6	–	–
D2L–Second dorsal-fin length	12.3	12.1	12.9	12.5	12.5	13.5	13.9
D2A–Second dorsal-fin anterior margin	11.3	10.8	11.5	11.1	–	–	–
D2B–Second dorsal-fin base	9.1	8.7	9.2	8.9	8.8	9.4	10.2

Table 1. cont'd.

	O. leptolineatus sp. nov.				*O. japonicus*		
		Paratypes (n = 5)				Non-types (n = 2)	
	Holotype	Min.	Max.	Mean	Syntype	Min	Max
D2H–Second dorsal-fin height	8.5	7.7	8.6	8.0	7.3	7.8	7.8
D2I–Second dorsal-fin inner margin	3.9	3.6	4.0	3.8	4.0	3.9	4.4
D2P–Second dorsal-fin posterior margin	8.6	7.8	8.8	8.2	7.1	–	–
ANL–Anal-fin length	8.3	9.9	10.9	10.3	9.4	–	–
ANA–Anal-fin anterior margin	8.7	9.5	11.0	10.1	8.8	–	–
ANB–Anal-fin base	5.9	7.0	8.0	7.7	7.2	–	–
ANH–Anal-fin height	3.8	3.5	4.5	4.1	4.3	–	–
ANI–Anal-fin inner margin	2.1	2.2	2.6	2.4	2.0	–	–
ANP–Anal-fin posterior margin	3.1	3.2	3.5	3.3	3.9	–	–
CDM–Dorsal caudal margin	21.4	19.4	22.2	21.1	21.8	20.4	21.8
CPV–Preventral caudal margin	16.6	15.0	16.3	15.7	–	–	–
CST–Subterminal caudal margin	3.4	2.6	3.7	3.3	3.3	–	–
CTR–Terminal caudal margin	6.4	5.6	6.5	6.0	6.0	–	–
CTL–Terminal caudal lobe	7.0	5.5	7.1	6.4	6.5	–	–
P1L–Pectoral-fin length	16.7	15.2	16.9	16.1	–	–	–
P1A–Pectoral-fin anterior margin	17.4	18.0	19.3	18.9	17.2	16.0	18.9
P1B–Pectoral-fin base	9.0	10.0	11.3	10.5	8.7	9.7	11.0
P1H–Pectoral-fin height	12.2	13.2	14.7	14.0	13.4	–	–
P1I–Pectoral-fin inner margin	4.8	3.8	5.0	4.2	5.3	5.0	5.4
P1P–Pectoral-fin posterior margin	11.6	12.6	14.5	13.6	11.8	12.3	13.5
P2L–Pelvic-fin length	14.8	13.2	15.9	14.7	13.6	13.9	14.1
P2A–Pelvic-fin anterior margin	11.1	10.5	11.9	11.1	10.6	11.1	11.2
P2B–Pelvic-fin base	9.5	9.4	10.8	9.9	9.5	–	–
P2H–Pelvic-fin height	7.3	8.1	9.8	8.8	9.3	–	–
P2I–Pelvic-fin inner margin	5.4	3.9	6.4	5.3	4.5	–	–
P2P–Pelvic-fin posterior margin	9.5	8.9	10.3	9.7	8.2	–	–
CLO-Clasper outer length	10.7	8.9	9.9	9.2	–	–	–
CLI-Clasper inner length	15.4	14.2	16.3	15.0	–	–	–
CLB-Clasper base width	2.9	2.2	2.9	2.6	–	–	–
HDH–Head height (at eye)	7.4	6.2	8.5	7.4	6.4	–	–
HDW–Head width (at eye)	15.4	15.9	16.7	16.2	14.9	–	–
TRH–Trunk height	10.0	9.8	14.9	12.3	8.8	–	–
TRW–Trunk width	16.8	16.4	20.2	17.3	15.1	–	–
CPHd–Caudal peduncle height (D2 insert)	3.7	3.5	4.2	3.8	3.9	–	–
CPHc–Caudal peduncle height (anal-fin insertion)	3.3	2.9	3.6	3.3	3.4	–	–
CPWd–Caudal peduncle width (D2 insert)	3.8	3.4	4.1	3.8	3.1	–	–
CPWc–Caudal peduncle width (anal-fin insertion)	2.5	2.1	2.4	2.3	1.9	–	–
DPI–First dorsal midpoint–pectoral insertion	24.8	23.0	29.6	27.1	24.6	–	–
DPO–First dorsal midpoint–pelvic origin	9.5	10.0	12.2	11.1	9.8	–	–
DAO–Second dorsal origin–anal origin	10.4	8.6	10.7	9.6	9.5	–	–
DAI–Second dorsal insert.–anal insert.	8.0	7.3	8.6	7.8	7.1	–	–
PPS–Pectoral–pelvic space	18.4	14.7	19.8	17.6	16.4	14.7	17.5
PAS–Pelvic–anal space	23.1	19.2	23.1	20.8	20.6	20.2	20.4
PCA–Pelvic–caudal space	26.9	26.4	31.0	28.3	27.4	–	–

Figure 3. Underwater image of a specimen of *Orectolobus leptolineatus* sp. nov. photographed *in situ* on a coral reef at Silayukti Point on Bali's east coast at about 20 m depth (specimen not collected). Photograph by Mike Severns.

slightly distally, cartilage at glans opening sharp-edged. Dorsal fins similar in shape, stiff, subtriangular, upright, first slightly larger than second, height of first 1.12 (1.15–1.22) times height of second, with almost straight anterior margins; apices narrowly rounded; posterior margins slightly concave (almost straight in some paratypes), margin almost vertical to directed slightly anterodorsally from free rear tip; inner margin usually parallel to dorsal surface with free rear tip bluntly angular; first dorsal-fin origin usually slightly anterior to pelvic-fin insertion (in paratype CSIRO H 5787–02, about over posterior third of pelvic-fin base), second originating well behind rear tip of pelvic fin (sometimes over tip of clasper in adult males); first dorsal-fin inner margin 1.28 (1.19–1.52) times spiracle length. Pectoral fin large, base fleshy, length 16.7 (15.2–16.9)% TL; anterior margin moderately convex, 3.60 (3.71–5.09) times inner margin; apex narrowly rounded, posterior margin weakly S-shaped (nearly straight in some paratypes); inner margin convex (very strongly convex in some paratypes), free rear tip broadly rounded. Pelvic fins large, length 14.8 (13.2–15.9)% TL; anterior margin weakly convex, apex broadly rounded; posterior margin weakly to moderately convex; inner margin almost straight (concave in some paratypes), free rear tip narrowly rounded (broader in large females); pelvic-fin origin well forward of dorsal fins, origin to midpoint of first dorsal fin 9.5 (10.0–12.2)% TL. Anal fin strongly raked, elongate, lobe-like, well developed; base short, its length 5.9 (7.0–8.0)% TL, 0.84 (0.52–0.71) in interdorsal space; posterior margin almost vertical; origin behind insertion of second dorsal-fin but forward of its free-rear tip, anal-fin height 1.54 (1.58–2.29) in base length; anal-fin length 2.68 (2.81–3.30) times posterior margin length; inner margin length 0.68 (0.69–0.82) of posterior margin length. Caudal fin relatively elongate, dorsal caudal margin length 21.4 (19.4–22.2)% TL; origin of upper lobe not abrupt; lower lobe well developed, outer margin very strongly convex, united at its origin to insertion of anal fin, deeply notched at junction of terminal lobe; terminal lobe deep, outer margin very irregular, almost bilobed, length 2.11 (1.80–2.39) times spiracle length.

Spiral valve count 25 (n = 1, paratype CSIRO H 5787–01). Vertebral counts, n = 8: holotype (7 paratypes): monospondylous centra 51 (44–51); precaudal centra 111 (100–107); caudal centra 52 (47–51); total centra about 163 (148–156).

COLORATION.— Based on female paratype CSIRO H 5876–03, when fresh (Fig. 2a): Dorsal and lateral surfaces of body with a dense and very complex pattern of fine, pale vermiculations on a darker reddish brown body coloration (extending over both light and dark areas); dark markings (saddles and blotches) spaced irregularly with very diffuse edges; predorsal region with four, dark

Figure 4. Lateral view of tail: A. *Orectolobus leptolineatus* sp. nov., adult male holotype (MZB 18623, 887 mm TL, preserved), B. *Orectolobus japonicus* female syntype (BMNH 1862.11.1.18, 753 mm TL, preserved).

brown saddles (typically less prominent than in other wobbegong species), first saddle on head behind eyes V-shaped, second above pectoral-fin base, third centred over abdomen, and a smaller, less distinct saddle before first dorsal fin; lateral margins of first and second saddles with posteroventral extensions; additional dark brownish bars beneath each dorsal fin, their posterior edges about level with rear tip of dorsal fins, coalescing or almost so on ventral surface; single bar interdorsally, less distinct than those adjacent, almost coalescing ventrally; three elongate dark saddles on dorsal caudal margin, first centred over anal fin, second over ventral lobe and third over terminal lobe; saddles on trunk each bordered anteriorly and posteriorly by three, obscure reticulated ocelli (these blend into pale interspaces between saddles), additional ocelli distributed mid-laterally on flank; snout, orbital membrane and interorbital densely covered with fine vermiculations; vermiculations covering dorsal and caudal fins; dorsal surfaces of paired fins similar to body, equally well vermiculated; posterior edge of spiracle bordered by a large silvery white spot (approximately half eye-length). Ventral surface whitish, dusky in some large paratypes; some types with fine dark flecks where volcanic sand remains trapped beneath denticle cusps; ventral tail with subdorsal bars evident; outer half of pectoral fin often with a weak vermicular pattern; dermal lobes pale. After preservation, female paratype CSIRO H 5876–03: Dorsal ocelli becoming less distinct; vermiculations on pectoral and pelvic fins more pronounced than on the rest of the body. Other preserved specimens with equally complex vermicular colour patterns; base coloration varying from greyish brown to brownish.

MZB 18623, adult male holotype (Fig. 1), when preserved: Base colour darker than female paratype described above; ocelli-like markings more stellate with a single dark inner spot (similar to female paratype Indo–Oz L154, 436 mm TL, than larger female paratypes); vermiculations on paired fins of holotype slightly coarser than female paratype. Clasper dusky ventrally; some darker patches present dorsally.

Indo–Oz L154, juvenile female paratype, 436 mm TL, when fresh (Fig 2b): Similar pattern to large female, but vermiculations much coarser and fin coloration less complex and more diffuse. Ocelli bordering the dark dorsal saddles usually containing a single dark inner spot (compared to light and dark reticulations within ocelli of large specimens). Ventrally, differs from larger types by presence of obscure dusky spots on lower jaw.

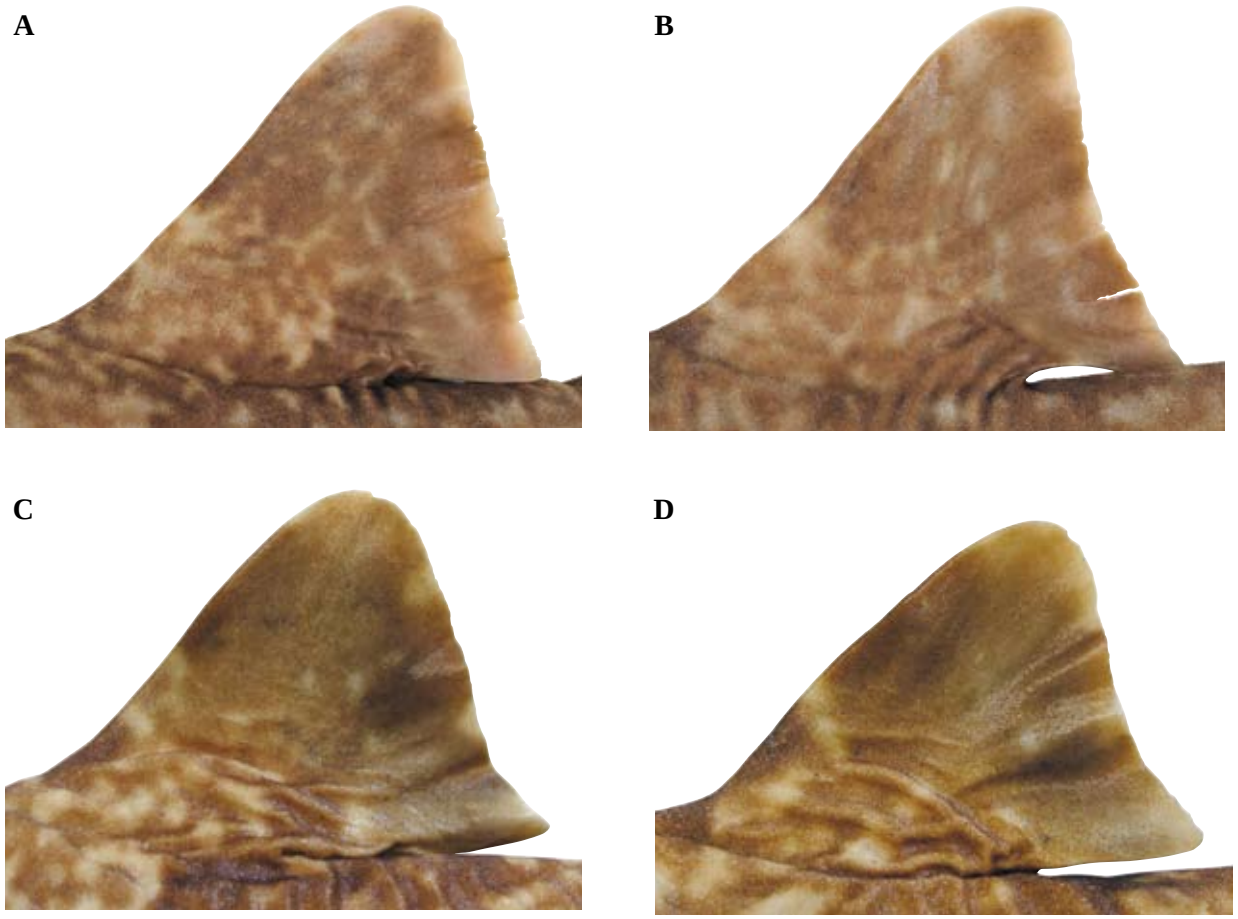

Figure 5. Dorsal-fin shapes of *Orectolobus leptolineatus* sp. nov., adult male holotype (MZB 18623, 887 mm TL, preserved): A. first dorsal fin; B. second dorsal fin. *Orectolobus japonicus* female syntype (BMNH 1862.11.1.18, 753 mm TL, preserved). C. first dorsal fin; D. second dorsal fin.

CSIRO H 6446–03, female mid-term embryo, 1 of 2 specimens, 140 mm TL, when fresh (Fig. 6a): no evidence of vermiculations or reticulations. Dark dorsal saddles and bars usually bordered by diffuse-edged, white spots, more evident anteriorly; darkest over origin of dorsal caudal margin; interorbit with four dark, obscure spots arranged as corners of a square; fins lacking a distinctive colour pattern, but occasional dark spots present, most obvious at dorsal-fin origins, near apices of dorsal fins and on outer margins of pectoral fins. After preservation, CSIRO H 6446–03 (Fig. 6b): white spots and bordering dorsal bars and saddles becoming much more pronounced than when fresh.

SIZE.— Females to at least 120 cm TL (n=35), males to at least 112 cm TL (n=48); one male adolescent at 89 cm TL (a non-type late adolescent at 87 cm TL); all males (n = 43) mature by ca 90 cm TL; smallest mature female recorded at 94 cm TL, two pregnant females recorded at 104 and 108 cm TL, smaller of the two pregnant females contained four mid-term embryos between 13 and 14 cm TL.

DISTRIBUTION.— Types were collected from fish landing sites at Jimbaran Bay (Kedonganan, south-west Bali) and Tanjung Luar (south-east Lombok). Although specific localities of capture of these specimens are unknown, they were caught near these landing sites. An live individual was also photographed *in situ* on a coral reef at Silayukti Point on Bali's east coast at about 20 m depth (Fig. 3); the same individual was apparently observed on multiple occasions (Pickell & Siagian, 2000). This species has also been photographed at a fish market in Pelabuhanratu (West Java, Indonesia). Its depth range is not well defined; specimens observed at fish markets in Indonesia were presumably caught by longline fishers operating in deeper parts of the continental shelf (i.e. landed with *Squalus* and triakid species which are most commonly found offshore on the outer continental shelf and upper slope). Probably prefers deeper colder water with the single shallow water observation from the east coast of Bali where cold-water upwelling is common (see Pickell & Siagian, 2000).

An image of a specimen collected off Sarawak in

Figure 6. Dorsal view of *Orectolobus leptolineatus* sp. nov., embryo paratype (CSIRO 6446–03 [1 of 2], female 140 mm TL): A, fresh; B. preserved.

Malaysian Borneo (Yano *et al*., 2005) appears to be this species. Similar, possibly conspecific, colour forms have been obtained from off southeastern Sabah, the Philippines (Visayas and Cebu City), Taiwan (Penghu Islands), and the Okinawa region of Japan (Fig. 8). There are additional literature records of '*O. japonicus*' from other localities in the Western Pacific, including Vietnam (Fourmanoir, 1965) and Korea (Mori, 1952), but the lack of images and/or specimens for these records prevents verification of their identity.

ETYMOLOGY.— Derived from a combination of the Greek *leptos* (fine, thin) and Latin *lineatus* (of a line) with reference to the thin, vermicular markings on the dorsal surface. Proposed vernacular name: 'Indonesian Wobbegong'.

REMARKS.— A number of recent taxonomic papers on Australian orectolobids, e.g. Last *et al*., (2006), Huveneers (2006), Last & Chidlow (2008), and an identification guide to the sharks and rays of Australia (Last & Stevens, 2009), have provided detailed information to discriminate Australian wobbegong species. Other than *O. leptolineatus*, *O. japonicus* is the only valid *Orectolobus* species known to occur outside of Australasia. *Orectolobus leptolineatus* has been confused in the literature with *O. maculatus* (e.g. Pickell & Siagian, 2000; Yano *et al*., 2005) and probably *O. japonicus* (e.g. colour form of Shen, 1993, pl. 3.10; Goto, 2008, in part: Okinawa specimens), presumably because of their superficially similar coloration. *Orectolobus leptolineatus* is possibly sympatric with *O. japonicus*, but allopatric with *O. maculatus*, which is confined to southern Australian waters and attains a larger size (ca 170 cm vs. ca 120 cm for *O. leptolineatus*).

The number of available morphometric specimens of *Orectolobus leptolineatus* (n=6) and *O. japonicus* (n=3) was small but these species appear to differ in the following body ratios: a longer prepectoral length (19.9–22.2% in *O. leptolineatus* vs. 17.4–19.8% TL in *O. japonicus*), longer head (length 22.9–24.7% vs. 21.3–22.1% TL), longer prebranchial length (17.6–19.3% vs. 16.6–17.3% TL), longer prespiracular length (9.3–10.0% vs. 8.5–9.2% TL), wider intereye space (7.0–7.5% vs. 6.7–6.9% TL), larger eye-spiracle space (1.8–2.2% vs. 1.6–1.7% TL), wider internarial space (5.0–5.4% vs. 4.7–5.0% TL), and slightly larger mouth (width 10.9–11.6% vs. 10.7% TL, n=1). *Orectolobus leptolineatus* types differ slightly from the syntype of *O. japonicus* in other characters: caudal-peduncle height 1.31–1.58 (rather than 1.79 in *O. japonicus*) times its width at anal-fin insertion; anal-fin length 2.68–3.30 (rather than 2.39) times its posterior margin; and anal-fin inner margin 0.68–0.82 (rather than 0.51) of its posterior margin.

The colorations of *O. leptolineatus* and *O. japonicus*, both having complex patterns of pale and dark blotches and

saddles edged with pale ocelli, are superficially similar. However, *O. leptolineatus* is typically paler with much denser reticulations and vermiculations on both the body and fins than *O. japonicus*. The extent of these differences appears more pronounced in adults than juveniles. Three large male specimens (865–904 mm TL) from Okinawa (HUMZ 162461, HUMZ 163200, HUMZ 163201) share a similar colour pattern with *O. leptolineatus* and fit well within the range of morphometrics for types of the new species. However, they were excluded from the type series as a precautionary measure, given the taxonomic complexities of this group and possible existence of a species-complex in the western North Pacific; along with other non-Indonesian specimens mentioned below, they are provisionally identified as *Orectolobus* cf. *leptolineatus* (see comparative material at the end of paper).

Other non-Indonesian specimens differ in morphometry and/or colour to the types. A specimen from the Philippines (SUML F 1079) has a colour pattern intermediate between *O. leptolineatus* and *O. japonicus*, but its morphometrics are most similar to *O. japonicus*. Another dried specimen from Borneo (CSIRO H 7112–01) has a similar colour pattern to the Philippines specimen. Other differences in coloration exist between *O. leptolineatus* and a specimen from Taiwan (AMS I 43794–002), but morphometrics were not taken as the specimen was twisted into a circular shape.

Goto (2008) demonstrated that Masuda *et al.*'s (1975) record of '*O. ornatus*' from Honshu (Japan) (SMBL F 74013) was conspecific with *O. japonicus*; the morphometry of this specimen concurs with his determination. Although the aberrant colour pattern is unique to this specimen, of the body measurements listed above to separate *O. japonicus* from *O. leptolineatus*, 8 out of 9 measurements agree with *O. japonicus*.

Figure 7. Dried skin and jaws (finless) of *Orectolobus* cf. *leptolineatus*, CSIRO H 7112–01, ca. 700 mm TL.

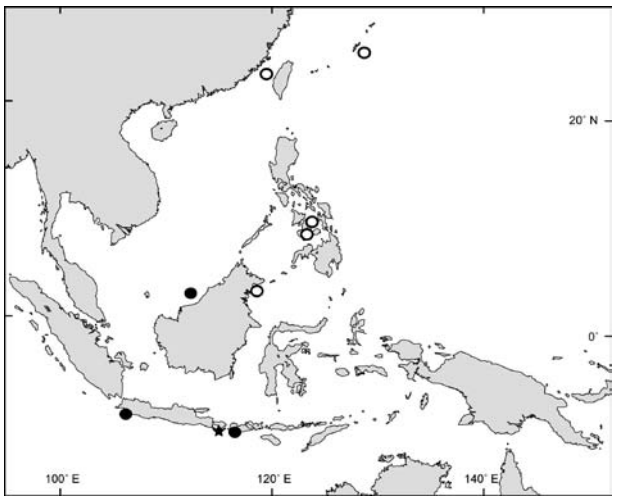

Figure 8. Distribution of *Orectolobus leptolineatus* sp. nov. in the Western Central Pacific. Solid star represents holotype, solid circles represent confirmed records and open circles represent records referred to as *O.* cf. *leptolineatus*.

Published distributional ranges of *O. japonicus* (e.g. see Goto, 2008) may be in incorrect due to possible confusion with *O. leptolineatus*. *Orectolobus leptolineatus* is known to occur off eastern Indonesia (Bali and Lombok), but confirmed images of the species have also been taken from southern Indonesia (West Java) and Malaysia (Sarawak). Specimens or images, possibly conspecific with *O. leptolineatus*, were examined from Malaysia (Sabah), the Philippines (Cebu), Taiwan (Penghu Islands) and the Okinawa Islands (southern Japan). In Japan, *O. japonicus* has been confirmed from Honshu, but also possibly occurs northwards to Hokkaido (HUMZ 116361, not seen) and southwards to Shikoku, Kyushu and the Amami Islands (Goto, 2008). Shen (1993) figured *O. japonicus* (as *O. maculatus*) in Fishes of Taiwan so, although we have not confirmed the source locality of this image, *O. japonicus* possibly occurs further south. The distributional ranges of these species may be influenced by the Kuroshio Current that flows northwards from the Philippines to southern Japan (see Motomura *et al*., 2010), but this is unlikely given their life history strategy and strong preference for benthic habitats of continental and insular shelves.

Huveneers (2006) successfully used spiral-valve counts to distinguish *O. halei* from *O. ornatus*. Goto (2008) recorded 23 spiral valves from the syntype of *O. japonicus* (BMNH 1862.11.1.18, Goto, pers. comm.); 25 spiral valves were counted from a single individual of *O. leptolineatus* in this study. Hence, based on the limited specimens examined, this character does not appear to be useful for distinguishing *O. leptolineatus* and *O. japonicus*, but additional work is warranted to be sure.

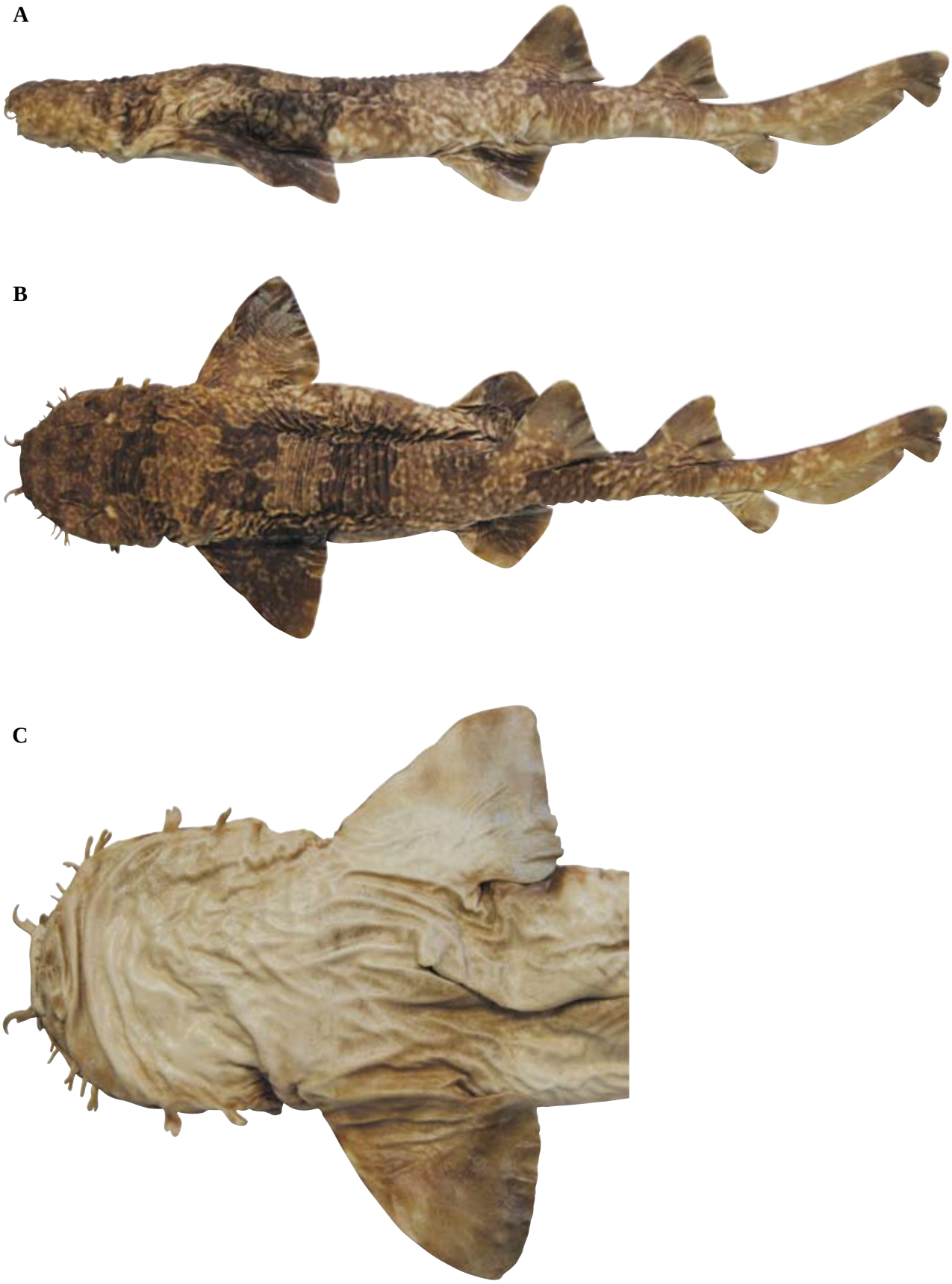

Figure 9. *Orectolobus japonicus* female syntype (BMNH 1862.11.1.18, 753 mm TL, preserved): A. lateral view; B. dorsal view; C. ventral view of head.

Interestingly, Corrigan & Beheregaray (2009) noted that specific status for *O. leptolineatus* (as *O*. cf. *ornatus*) was not supported by their molecular analyses. Their corrected sequence divergence between *O*. cf. *ornatus* and sister taxon *O. japonicus* was only 0.3%, well within the range of intraspecific variation for other species of wobbegongs. However, the caveat to this remark is that their '*O. japonicus*' specimen (AMS I 43794–002) is now regarded by the current authors to be more closely aligned with *O. leptolineatus* than *O. japonicus*, based on its colour pattern. Unfortunately, we have been unable to source genetic material from Japanese specimens at this stage. A detailed molecular study to further the work of Corrigan & Beheregaray (2009) is required to resolve the taxonomic problems in what may be a complex of similar species in the western North Pacific. Morphological and meristic variations also require further research, so fresh wobbegong specimens and their associated tissues need to be accessed widely from across this region.

Comparative material.
Orectolobus cf. *leptolineatus*: 6 specimens. AMS I 43794–002, female ca. 1020 mm TL, Makung fish market, Penghu Islands, Tawian, ca. 23º34′ N, 119°34′ E, 26 May 2005; CSIRO H 7112–01, dried skin and jaws, finless, ca.700 mm TL, Semporna fish market, east Sabah, Malaysia, 1996; HUMZ 162461, adult male 898 mm TL, Okinawa Prefecture, Japan, 10 Jul. 1999; HUMZ 163200, late adolescent male 865 mm TL, HUMZ 163201, adult male 904 mm TL, Okinawa Prefecture, Japan, 14 Aug. 1999; SUML F 1079 (formerly JPAG 0129), female 888 mm TL, Pasil fish market, Cebu, Philippines, ca. 10º17′ N, 123º53′ E, 20 Apr. 1999.
Orectolobus japonicus: 4 specimens. BMNH 1862.11.1.18 (syntype), female 753 mm TL, Japan, 1862; HUMZ 124403, immature male 538 mm TL; HUMZ 122404, female 1018 mm TL, off Shimoda, Shizuoka Prefecture, Honshu Island, Japan, Apr. 1992; SMBL F 74013, female 1039 mm TL, Tanabe Bay, Wayakama Prefecture, Honshu Island, Japan, 30 Apr. 1974.

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Rediscovery of the rare and endangered Borneo Shark *Carcharhinus borneensis* (Bleeker, 1858) (Carcharhiniformes: Carcharhinidae)

William T. White[1], Peter R. Last[1] & Annie P.K. Lim[2]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Fisheries Biosecurity Centre Sarawak, Jalan Buruh, 93450, Kuching, Sarawak, MALAYSIA

ABSTRACT.— *Carcharhinus borneensis* is considered to be one of the rarest and most poorly known carcharhinid sharks, previously only known from five valid specimens, all of which are juveniles. During recent surveys of the shark and ray fauna of Borneo, a moderately large number of specimens were recorded from one locality off Sarawak. *Carcharhinus borneensis* is a small species which differs from its congeners in having a long snout, a row of enlarged hyomandibular pores along each mouth corner, the second dorsal-fin origin situated above the anal-fin midbase, and the upper anterior teeth with narrow, oblique cusps and strong lateral cusplets. This species appears to have a very restricted range and actions to conserve it in the small area it occurs are urgently required.

Key words: *Carcharhinus borneensis* – Endangered – Borneo – rediscovered – restricted

PDF contact: william.white@csiro.au

INTRODUCTION

The Borneo Shark *Carcharhinus borneensis* was described by Pieter Bleeker in 1858 as *Carcharias* (*Prionodon*) *borneensis* based on a single specimen (immature male 249 mm TL) collected off Singkawang in East Kalimantan (Indonesian Borneo). Fowler (1941) placed this species in the genus *Eulamia*, which was proposed by Gill (1862) for *E. milberti* (= *C. plumbeus* (Nardo)) and synonomised with *Carcharhinus* by subsequent authors. Compagno (1979, 1988) examined a 469 mm immature female of *C. borneensis* from off Chu Shan Island in the Chekiang Province of China. Casto de Elera (1895) included this species in his catalogue of the fauna of the Philippines from Borongan in the Samar Province, without reference to specimens. However, Herre (1953) excluded this species in his checklist of Philippine fishes, and a recent WWF elasmobranch biodiversity survey also did not find any Philippine material of this species (Compagno *et al*., 2005b). Thus, there are no validated records of this species from the Philippine Archipelago and its distribution in this region is questionable. Similarly, Giltay (1933) recorded this species from Java but insufficient information was provided to validate this record.

In his detailed systematic account of the Carcharhiniformes, Compagno (1988) placed *C. borneensis* into the 'porosus' group, which also contains *C. porosus* (Ranzani), *C. dussumieri* (Müller & Henle), *C. sealei* (Pietschmann), *C. sorrah* (Müller & Henle), *C. hemiodon* (Müller & Henle), *C. macloti* (Müller & Henle), *C.* sp. A [*sensu* Compagno *et al*., 2005a] and possibly *C. fitzroyensis* (Whitley). These are all small species, typically with elongate, narrowly rounded snouts and upper teeth with narrow, oblique cusps, deeply notched postlateral edges and strong postlateral cusplets (Compagno, 1979, 1988). According to Garrick (1982), *C. borneensis* is unique compared to its congeners in having a discrete series of enlarged pores along each side of the mouth which corresponds more closely to the genus *Rhizoprionodon*, but it differs from this genus in its dentition and cranial anatomy (see Compagno, 1988). He also states that it is unique in possessing diplospondylous vertebrae occurring slightly in front of the pelvic origin.

Carcharhinus borneensis was listed as Endangered by the *IUCN Red List of Threatened Animals* (Compagno, 2005), based on the fact that only five specimens (four from Borneo, one from China) have been recorded up to 1937, and none since, in a heavily fished region. This species was not recorded in a survey of the sharks in fish markets of Sabah organised under the UK Darwin Initiative program in 1996/1997 (Compagno, 2005). However, during investigation of sharks for the Malaysian National Plan of Action for sharks (NPOA), specimens

of *C. borneensis* were recorded from Mukah in Sarawak in early April 2004. During subsequent trips in late April and May 2004, as part of a comprehensive survey of the fish markets around the whole island of Borneo funded largely by the National Science Foundation, more specimens of *C. borneensis* were recorded from the same locality. A total of 11 *C. borneensis* were retained in collections. Yano *et al*. (2005) included *C. borneensis* in their guide to Malaysian sharks and rays based on some 18 specimens collected off Borneo. Although information provided in this account mostly refers to this species, it appears to be synthesised from earlier work of Compagno (1979) and Garrick (1982). Furthermore, the specimen figured clearly refers to *Rhizoprionodon acutus*, not *C. borneensis*, based on the length of the labial furrows and more posteriorly located second dorsal fin. Also, vertebral counts they included are much higher than those recorded for *C. borneensis* by Garrick (1982), i.e. 131–133 vs. 118–121, which are closer to *R. acutus*, i.e. 121–162 (Springer, 1964). Yano et al. (2005) also made a similar misidentification of another carcharhinid (as *Carcharhinus* sp., p 243) which they stated as being similar to their *C. borneensis*; in this case, the specimen figured is most likely *Rhizoprionodon oligolinx*. Unfortunately, these misidentifications have added confusion to the literature, especially in the case of *C. borneensis*.

The present account compares the recent material of *C. borneensis* collected from surveys of fish landing sites in Borneo with the historic specimens detailed in Garrick (1982). Fresh images and a colour description of *C. borneensis* are provided for the first time, and a redescription is provided based on adult and juvenile material.

METHODS

Measurement terminology follows Compagno (1984, 1988, 2001) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Direct measurements were used unless specified otherwise. Some measurements, e.g. head length, were also taken horizontally to account for different measurement protocols followed by other researchers. Dentitional terms generally follow Compagno (1979, 1988, 2001). Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1979, 1988, 2001).

The holotype and 12 specimens of *Carcharhinus borneensis*, including 11 recently collected specimens, were measured in full (Table 1). Although Garrick (1982) stated that the holotype of *C. borneensis* was not suitable for providing accurate measurements, a visit to the Leiden museum (November 2009) by the senior author determined the holotype could be relatively accurately measured despite its somewhat flabby condition. Morphometric and meristic values are supplied as ranges in the descriptive section. Meristics were taken from radiographs of three of the recently collected specimens of *C. borneensis* and compared to the four provided in Garrick (1982). Counts were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of upper lobe of caudal fin) and caudal (centra of the caudal fin) vertebrae (Table 2). Tooth row counts were taken in situ from the holotype and two of the recently collected specimens and combined with the counts provided by Garrick (1982) for RMNH 7666, BMNH 1895.2.28 and SU 66750. In the description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the other specimens. The redescription is based primarily on the recently collected specimens because they are in better condition than the holotype.

Specimens are referred to by the following prefixes for their registration numbers: CSIRO, Australian National Fish Collection, Hobart; RMNH, Rikjsmuseum van Natuurlkjke Histoire, Leiden; SU, Stanford University housed at the California Academy of Sciences (CAS), California; BMNH, British Museum of Natural History, London; IPPS, Institut Penyelidikan Perikanan Sarawak (Sarawak Fisheries Research Institute), Kuching, Sarawak.

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus *Carcharhinus* Blainville, 1816

Type species. *Carcharias melanopterus* Quoy & Gaimard, 1824, under suspension of the Rules by the ICZN, Opinion 723, 1965, Bull. Zool. Nomencl. 22: 32.

SPECIES.— *Carcharhinus* includes at least 30 nominal species (see Compagno *et al*., 2005a) and one undescribed species, *C*. sp. A [*sensu* Compagno *et al*., 2005a].

Carcharhinus borneensis (Bleeker, 1858)

Figs 1–6; Tables 1, 2

Carcharias (*Prionodon*) *borneensis* Bleeker, 1858: 8 (Type locality: Singkawang, Borneo).

Holotype. RMNH 7386, immature male 237 mm TL (fresh umbilical scar present), Singkawang, West Kalimantan, Indonesia.

Other material examined. 12 specimens: CSIRO H 6226–01, juvenile male 341 mm TL, CSIRO H 6226–02, female 348 mm TL, IPPS 53/07, juvenile male 343 mm TL, IPPS 47/07, juvenile male 373 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E,

Figure 1. Lateral view (A) and ventral view of head (B) of the holotype of *Carcharhinus borneensis* RMNH 7386 (immature male 237 mm TL).

08 Apr. 2004; CSIRO H 6212–01, adult male 576 mm TL, IPPS BO428, adult male 574 mm TL, IPPS BO426, adult male 575 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 27 Apr. 2004; IPPS BO456, female 618 mm TL, IPPS BO449, female 601 mm TL, IPPS BO459, adult female 578 mm TL, IPPS 28404–13, female 596 mm TL, 02°53.52′ N, 112°05.44′ E, 28 Apr. 2004; RMNH 7666, juvenile female 275 mm TL (fresh umbilical scar present), Pontianak, West Kalimantan, Indonesia, 1895.

Other material not examined. 2 specimens: BMNH 1895.2.28, male 332 mm TL, Sarawak, Borneo; SU 66750, immature female 469 mm TL, Dinghai, Chu Shan (Zhousan) Island, Chekiang Province, China, January 1937 (cranium dissected).

DIAGNOSIS.— A small species of *Carcharhinus* with the following combination of characters: a long and pointed snout; slender body and tail; a row of enlarged hyomandibular pores (5–12) alongside each mouth corner; upper anterior teeth finely serrated with a single narrow, oblique cusp; distal edge deeply notched and with several cusplets; lower anterior teeth with narrower, similarly oblique cusps; no lateral cusplets; total tooth row counts 23–26/23–25, or 46–50; second dorsal-fin origin well posterior of anal-fin origin, about opposite or just anterior to anal-fin midbase, second dorsal-fin origin to anal-fin origin 2.2–4.1% TL, 0.4–0.9 times second dorsal-fin base; interdorsal space 20.7–22.7% TL; pelvic fins small, anterior margins 4.4–5.8% TL and 35–42% of pectoral anterior margin; first dorsal fin triangular, with nearly straight posterior margin, free rear tip about opposite pelvic-fin origins, length 14.5–17.6% TL, 1.8–2.4 times height, inner margin 1.9–2.8 in base; second dorsal fin much smaller than first, slightly smaller than anal fin; length 7.5–10.2% TL, base 2.0–3.1 times height; height 21–29% of first dorsal fin height; anal fin height 1.1–1.6 times second dorsal height, base 1.1–1.5 times second dorsal-fin base; total vertebral counts 117–121, monospondylous precaudal counts 33–36, diplospondylous precaudal counts 21–26, diplospondylous caudal counts 56–60, precaudal counts 57–63; colour slate-grey dorsally, whitish ventrally with waterline clearly demarcated along head and body, no distinct black markings on fins, pectoral fins and lower caudal lobe with whitish margins.

DESCRIPTION.— Body slender, trunk subcircular and almost pear-shaped in section at first dorsal-fin base, length of trunk from fifth gill slits to vent 0.96 in holotype

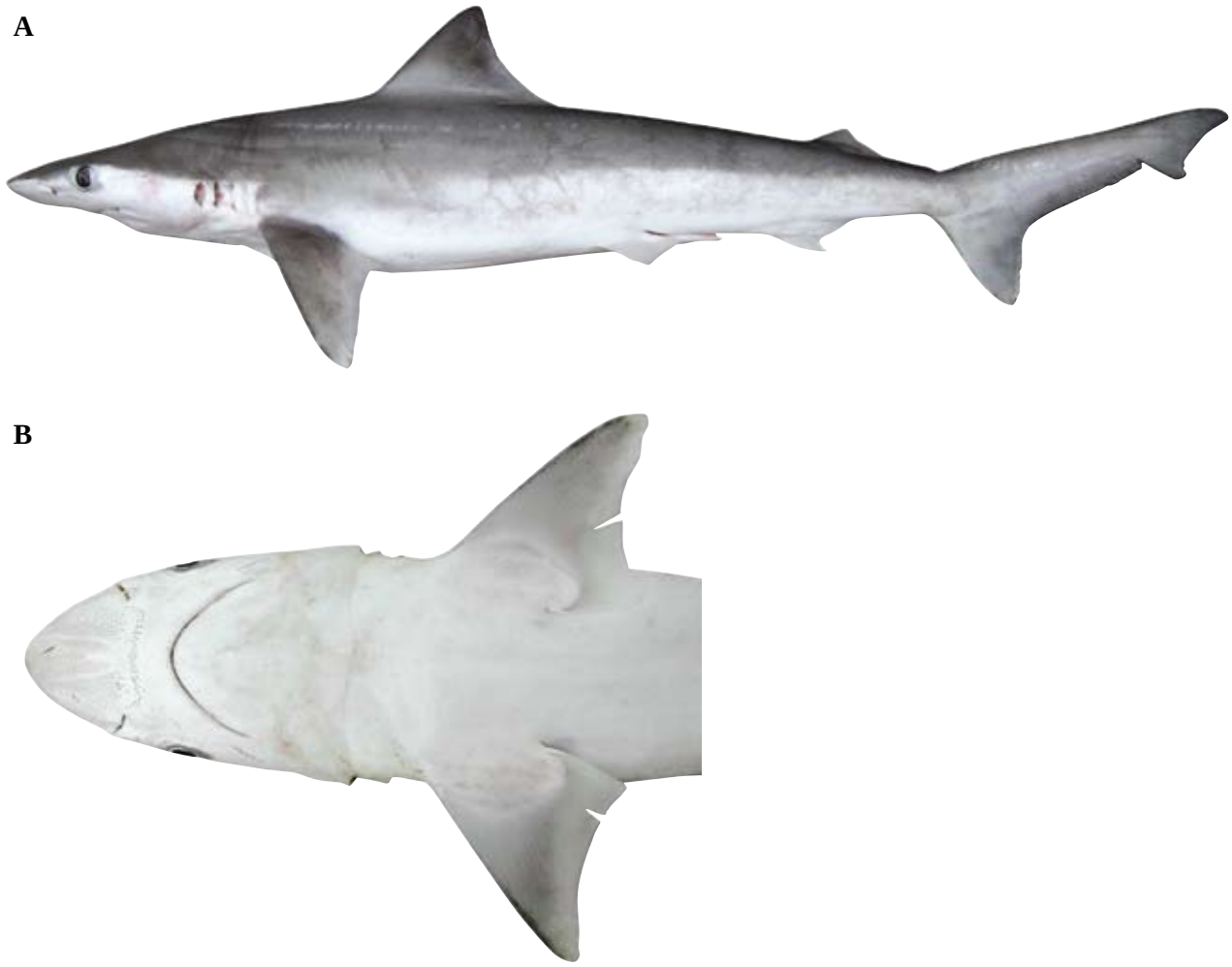

Figure 2. Lateral view (A) and ventral view of head (B) of a fresh adult specimen of *Carcharhinus borneensis* IPPS BO428 (adult male 574 mm TL).

(0.98–1.25 in 12 other specimens) times head length. Predorsal, interdorsal and postdorsal ridges absent from midline of back, lateral ridges absent from body. Caudal peduncle relatively slender, rounded-hexagonal in section at second dorsal-fin insertion, postdorsal and postventral spaces flattened and sometimes with a shallow median groove anteriorly, lateral surfaces subangular; height of caudal peduncle at second dorsal-fin insertion 1.51 (0.99–1.57) times its width, 1.80 (1.46–2.14) times in dorsal–caudal space. Precaudal pits present; upper pit a deep, arcuate and crescentic depression; lower pit a distinct, relatively shallow crescentic depression.

Head length to fifth gill opening 0.82 (0.74–0.94) times in pectoral–pelvic space. Head narrow and moderately flattened, ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, nearly straight on snout, weakly convex above eye, moderately concave at nape and convex above gills, weakly convex ventrally along lower jaws and beneath gills. In dorsoventral view, head anteriorly narrowly pointed; gill septa expanded slightly outwards. A discrete longitudinal row of 5–12 enlarged hyomandibular pores adjacent to each mouth corner. Snout long, preoral snout length 0.93 (0.99–1.17) times mouth width; tip pointed in dorsoventral view and noticeably indented anterior to nostrils; snout bluntly pointed in lateral view, nearly straight above to weakly convex above and convex below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, with height 0.97 (0.87–1.12) in eye length. Eyes moderately large, length 11.26 (10.00–15.08) in head length; situated laterally, with lower edges not crossing horizontal head rim in dorsal view; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

Spiracles absent. First two gill openings shortest, last

Table 1. Proportional dimensions as percentages of total length for the holotype (RMNH 7386) and 12 other specimens of *Carcharhinus borneensis*. The specimens are arranged in order of increasing size from left to right. Ranges all 13 specimens are also provided.

	RMNH 7386	RMNH 7666	CSIRO H 6226–01	IPPS 53/07	CSIRO H 6226–02	IPPS 47/07	IPPS BO428	IPPS BO426	CSIRO H 6212–01	IPPS BO459	SFRI 28404–13	IPPS BO449	IPPS BO456	**Min.**	**Max.**
TOT	237	275	341	343	348	373	574	575	576	578	596	601	618	237	618
PRC	76.2	76.1	73.9	73.8	72.7	72.9	75.1	74.6	73.6	73.9	74.3	73.4	73.9	72.7	76.2
PD2	63.8	63.0	62.5	62.1	61.4	61.7	62.2	61.9	60.9	61.4	61.6	62.4	61.2	60.9	63.8
PD1	31.8	29.8	30.9	30.4	30.9	29.9	30.1	28.9	27.5	28.9	28.3	29.0	28.4	27.5	31.8
HDL	26.5	24.3	24.8	24.2	24.6	24.6	22.6	23.6	23.2	22.8	23.8	22.3	22.8	22.3	26.5
PG1	20.2	20.2	20.8	20.4	20.3	20.7	18.8	19.6	19.3	19.0	19.6	18.4	19.1	18.4	20.8
POB	9.5	9.7	10.2	9.6	9.7	9.6	9.2	9.6	9.5	9.1	9.1	8.6	8.8	8.6	10.2
POB(horiz.)	7.7	8.1	8.0	8.7	8.0	9.0	7.8	8.1	8.0	7.6	8.0	7.3	7.9	7.3	9.0
POR	8.0	8.3	9.2	9.2	9.2	9.1	8.3	8.5	8.6	8.4	8.6	8.1	8.3	8.0	9.2
PRN	6.1	6.5	6.8	6.8	7.0	6.9	6.5	6.6	6.7	6.5	6.5	5.9	6.3	5.9	7.0
PRN(horiz.)	5.4	5.3	5.9	5.9	6.0	5.8	5.8	5.9	5.9	5.8	5.7	5.3	5.5	5.3	6.0
PP1	23.5	22.6	23.1	23.3	22.9	23.3	21.4	22.6	21.1	21.4	22.2	21.5	21.9	21.1	23.5
PP2	47.7	49.2	46.9	46.2	46.6	46.9	47.0	45.9	44.6	46.5	47.3	46.4	47.0	44.6	49.2
SVL	50.0	50.6	49.0	47.6	48.0	49.2	48.6	47.7	46.0	47.4	48.5	47.8	49.2	46.0	50.6
PAL	60.3	60.5	59.5	59.5	57.9	58.7	58.9	57.9	56.9	57.4	59.1	58.2	59.1	56.9	60.5
IDS	21.6	21.1	21.6	20.7	20.8	20.7	22.0	22.5	22.0	21.4	21.8	22.7	21.7	20.7	22.7
DCS	7.4	7.0	7.4	7.2	7.8	7.3	7.8	8.5	8.1	7.5	7.8	7.0	8.0	7.0	8.5
PPS	21.7	21.8	19.6	18.3	18.2	19.2	20.1	19.0	18.9	20.5	20.8	20.8	20.7	18.2	21.8
PAS	8.0	8.2	8.6	7.6	8.0	7.1	7.5	7.0	8.4	7.1	7.9	8.0	7.8	7.0	8.6
ACS	8.1	8.1	8.0	7.9	8.1	8.4	8.1	8.5	9.0	8.3	8.4	8.2	7.9	7.9	9.0
EYL	2.4	2.3	2.4	2.2	2.5	1.9	1.7	1.6	1.7	1.6	1.6	1.6	1.8	1.6	2.5
EYH	2.4	2.3	2.2	2.5	2.4	2.1	1.8	1.7	1.7	1.6	1.8	1.6	1.6	1.6	2.5
INO	9.5	10.5	10.4	9.8	10.0	10.0	9.4	9.4	9.3	9.0	9.2	8.9	9.2	8.9	10.5
NOW	1.8	2.0	2.0	1.9	1.9	1.7	1.6	1.5	1.5	1.6	1.5	1.5	1.3	1.5	2.0
INW	5.6	6.3	6.4	6.2	6.4	6.3	6.1	5.9	5.8	5.8	5.9	5.5	5.6	5.5	6.4
ANF	0.3	0.5	0.5	0.3	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.3	0.3	0.3	0.5
MOL	4.7	5.0	4.7	4.8	4.9	4.6	4.0	4.6	4.5	4.3	4.3	4.0	4.4	4.0	5.0
MOW	8.6	7.8	8.5	8.6	8.3	8.5	8.4	7.9	7.4	7.4	7.7	7.4	7.7	7.4	8.6
ULA	0.5	0.3	0.3	0.1	0.3	0.3	0.2	0.2	0.4	0.2	0.3	0.2	0.1	0.1	0.5
LLA	0.6	0.5	0.4	0.4	0.6	0.3	0.3	0.3	0.4	0.3	0.2	0.5	0.2	0.2	0.6
GS1	2.3	2.2	2.5	2.7	2.3	2.2	2.2	2.1	2.2	2.2	2.1	1.8	2.2	1.8	2.7
GS3	2.7	2.4	2.9	3.3	3.0	2.9	2.7	2.7	2.6	2.2	2.4	2.5	2.5	2.2	3.3
GS5	3.0	2.6	3.2	3.0	2.6	3.2	2.6	2.9	2.7	2.3	2.4	2.5	2.2	2.3	3.2
HDH	8.1	10.8	10.4	11.2	10.8	11.3	10.8	9.7	8.3	7.8	10.3	8.9	9.7	7.8	11.3
TRH	8.2	12.1	11.8	12.6	12.3	11.8	12.2	10.0	8.8	8.2	10.9	9.1	9.9	8.2	12.6
TAH	7.7	9.3	9.3	8.5	9.2	9.1	9.0	8.1	8.1	8.4	9.1	9.0	9.9	7.7	9.3
CPH	4.1	4.8	4.3	4.1	4.6	4.4	3.9	4.0	3.9	3.8	4.1	3.9	3.9	3.8	4.8
HDW	9.4	10.6	11.7	12.1	11.6	12.1	10.8	10.6	10.5	10.4	10.8	10.0	10.5	9.4	12.1
TRW	8.7	9.2	10.8	11.6	10.3	11.7	10.1	9.1	9.4	9.5	10.3	9.3	9.6	8.7	11.7
TAW	5.8	6.1	7.8	7.5	6.7	7.0	7.5	7.3	7.0	6.7	7.7	7.7	8.0	5.8	7.8
CPW	2.7	3.1	3.9	3.5	3.5	3.4	3.9	3.7	3.8	3.7	3.9	3.8	4.0	2.7	3.9
P1L	8.5	10.1	11.1	10.4	10.7	11.3	10.8	9.8	10.6	10.9	10.7	10.4	10.5	8.5	11.3
P1A	10.9	14.1	13.9	12.8	14.2	14.0	13.6	13.9	14.1	14.8	14.3	13.3	14.7	10.9	14.8

Table 1. cont'd.

	RMNH 7386	RMNH 7666	CSIRO H 6226–01	IPPS 53/07	CSIRO H 6226–02	IPPS 47/07	IPPS BO428	IPPS BO426	CSIRO H 6212–01	IPPS BO459	SFRI 28404–13	IPPS BO449	IPPS BO456	**Min.**	**Max.**
P1B	5.9	5.5	6.1	5.8	5.9	6.4	6.3	5.8	6.5	5.9	6.4	6.2	6.0	5.5	6.5
P1H	10.2	9.6	11.7	10.7	11.3	11.7	12.1	11.9	12.0	12.6	12.0	12.2	12.8	9.6	12.6
P1I	4.6	5.2	5.7	5.2	5.1	5.5	4.9	5.2	5.0	5.6	5.2	5.1	5.5	4.6	5.7
P1P	8.5	7.9	9.1	10.5	9.8	9.9	10.8	10.1	11.6	11.0	10.9	9.9	10.5	7.9	11.6
P2L	6.7	7.6	7.4	7.4	7.8	7.6	7.5	7.4	7.6	7.9	7.7	7.4	8.0	6.7	7.9
P2A	4.4	5.2	5.8	5.3	5.5	5.6	5.4	4.9	5.2	5.6	5.7	5.4	5.7	4.4	5.8
P2B	4.8	4.2	4.6	3.8	4.1	4.5	4.5	4.8	5.0	4.0	4.7	4.6	5.1	3.8	5.0
P2H	3.6	3.8	3.5	3.9	4.0	4.5	4.4	4.3	4.1	4.2	4.0	4.2	4.5	3.5	4.5
P2I	3.0	3.0	3.5	3.5	3.9	3.4	3.2	2.9	3.1	3.8	3.3	2.9	3.0	2.9	3.9
P2P	3.5	3.7	3.9	3.9	4.4	4.1	4.0	3.8	3.9	4.9	4.8	4.8	4.9	3.5	4.9
CLO	–	–	–	–	–	–	6.5	6.3	6.2	–	–	–	–	6.2	6.5
CLI	–	–	–	–	–	–	9.0	9.2	9.7	–	–	–	–	9.0	9.7
CLB	–	–	–	–	–	–	1.4	1.2	1.3	–	–	–	–	1.2	1.4
D1L	14.5	16.9	17.0	17.6	16.0	17.2	16.1	16.0	16.3	16.8	15.7	16.0	16.9	14.5	17.6
D1A	11.6	14.1	13.6	13.8	13.1	13.5	12.2	12.9	12.7	13.6	13.4	12.2	13.7	11.6	14.1
D1B	9.0	12.9	11.9	12.3	11.2	12.2	10.9	10.9	11.0	11.1	11.7	10.7	11.5	9.0	12.9
D1H	7.4	7.1	8.1	7.5	7.5	8.3	8.8	8.5	8.3	8.1	8.2	8.2	8.5	7.1	8.8
D1I	4.4	4.6	5.6	5.1	5.0	5.4	5.1	5.4	5.7	5.7	4.1	5.3	5.6	4.1	5.7
D1P	8.9	8.0	10.2	9.5	9.0	10.3	11.1	10.0	9.6	9.6	9.4	10.0	10.4	8.0	11.1
D2L	7.5	8.7	8.9	9.5	8.5	9.7	10.2	9.0	9.6	9.0	9.7	8.9	9.7	7.5	10.2
D2A	3.8	5.0	4.9	5.2	4.7	5.4	5.5	4.6	4.9	4.9	5.2	4.6	5.5	3.8	5.5
D2B	4.4	4.9	4.6	5.6	4.4	5.2	5.6	4.8	5.0	4.4	5.0	4.6	5.4	4.4	5.6
D2H	1.6	2.1	2.0	1.8	2.2	2.2	2.1	2.0	2.2	2.1	2.2	2.2	1.9	1.6	2.2
D2I	3.5	4.0	4.3	4.6	4.3	4.7	4.6	4.4	4.7	4.6	4.9	4.6	4.6	3.5	4.9
D2P	4.5	4.0	4.6	5.1	4.7	4.8	5.2	5.2	5.4	5.1	5.4	5.1	5.0	4.0	5.4
ANL	8.8	8.8	9.7	9.8	9.2	9.8	11.1	10.3	10.6	10.9	10.0	9.5	9.9	8.8	11.1
ANA	5.5	5.9	6.8	6.9	6.3	7.2	7.4	7.4	7.3	7.8	6.5	6.2	6.8	5.5	7.8
ANB	5.4	5.3	5.5	6.1	5.0	5.8	6.8	6.5	6.4	6.6	5.6	5.5	5.7	5.0	6.8
ANH	2.5	2.2	3.0	2.7	3.1	3.0	2.8	2.5	2.9	2.8	2.7	2.7	2.8	2.2	3.1
ANI	3.1	3.9	4.1	4.3	4.4	3.7	4.2	3.9	4.4	4.4	4.4	4.3	4.2	3.1	4.4
ANP	3.9	3.7	4.3	3.9	3.9	3.7	4.8	4.4	4.7	4.1	4.7	4.2	4.6	3.7	4.8
CDM	25.0	26.3	27.1	27.0	27.7	26.5	25.2	25.1	26.2	26.5	25.3	26.7	26.2	25.0	27.7
CPV	9.2	10.9	11.3	11.1	11.1	11.8	10.7	10.5	10.5	11.2	10.6	10.4	11.2	9.2	11.8
CPL	4.8	4.7	5.0	4.9	5.8	5.4	5.8	4.8	5.1	5.5	5.0	4.8	5.6	4.7	5.8
CPU	11.4	11.3	10.7	10.7	10.8	10.4	10.7	11.6	10.9	11.4	11.2	10.5	11.1	10.4	11.6
CFW	6.1	6.3	6.3	6.3	6.3	6.4	6.6	6.5	6.2	6.6	6.8	6.5	6.9	6.1	6.8
CFL	8.1	9.8	9.5	9.5	9.1	9.3	8.9	8.5	9.1	9.0	8.8	9.0	8.8	8.1	9.8
CST	3.3	4.4	4.4	4.9	4.8	4.2	4.4	3.7	3.8	4.6	3.7	4.2	4.1	3.3	4.9
CTR	5.8	5.1	6.5	5.9	6.6	6.5	6.7	6.8	6.9	7.0	6.6	7.3	7.0	5.1	7.3
CTL	6.7	8.6	8.8	9.0	8.9	8.6	8.7	8.4	8.6	8.8	8.1	9.4	8.8	6.7	9.4
DAO	2.3	2.4	3.0	3.1	3.4	2.8	3.4	4.1	3.5	4.1	2.5	3.6	2.2	2.3	4.1
DAI	1.7	1.4	1.7	1.6	2.2	1.9	1.8	1.6	1.9	2.2	1.8	2.7	1.3	1.4	2.7
DPI	8.9	8.4	7.2	7.3	7.0	6.4	7.9	6.9	7.7	7.0	7.6	8.2	7.0	6.4	8.9
DPO	10.3	12.1	10.8	10.4	9.8	10.2	11.1	10.9	10.5	12.1	12.7	11.4	12.9	9.8	12.7
PDI	8.0	9.2	8.2	7.1	7.6	7.2	9.1	8.1	7.9	8.6	9.8	8.7	10.3	7.1	9.8
PDO	12.9	11.0	13.6	12.3	12.9	12.5	12.6	13.3	13.6	12.7	12.0	13.6	11.5	11.0	13.6

three openings larger, subequal in height, fifth about 1.13 (0.84–1.11) of height of third; height of third about 9.83 (7.30–10.42) in head length and 1.15 (1.04–1.71) times eye length. Gill openings becoming slightly oblique posteriorly; margins of first four gill openings straight, posterior margins irregular; fifth weakly concave. Gill filaments not visible from outside. Upper end of highest gill opening about level with mid-eye. Gill-raker papillae absent from gill arches.

Nostrils strongly oblique, slit-like with large oval incurrent apertures; prominent triangular anterior nasal flaps with narrowly pointed tips, mesonarial flaps absent, small suboval excurrent apertures, posterior nasal flaps absent; well in front of mouth; width 3.08 (3.21–4.17) in internarial width, 1.30 (1.02–1.33) in eye length, 1.50 (1.33–2.02) in longest gill-opening.

Mouth broadly rounded and large; width 3.08 (2.70–3.16) in head length; mouth length 1.81 (1.56–2.11) in mouth width. Lips concealing teeth when mouth is closed. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve narrow, width much less than eye diameter, strongly papillose. No large buccal papillae on floor or roof of mouth behind maxillary valve. Palate, floor of mouth and gill arches covered with buccopharyngeal denticles. Labial furrows short, uppers 0.78 (0.38–1.73) times as long as lowers, lowers concealed by overlapping upper lip; anterior ends of uppers far behind eyes by distance of almost half of mouth width.

Teeth relatively few, 23 (25–26, n=5)/23 (23–25) rows or 46 (48–50) total rows (both jaws). Teeth not arranged in diagonal files, no toothless spaces at symphysis. Tooth formula (n=6): upper jaw 11 (12) + 1 (1) + 11 (11–12); lower jaw 11 (11–12) + 1 (1) + 11 (11–12). Upper teeth

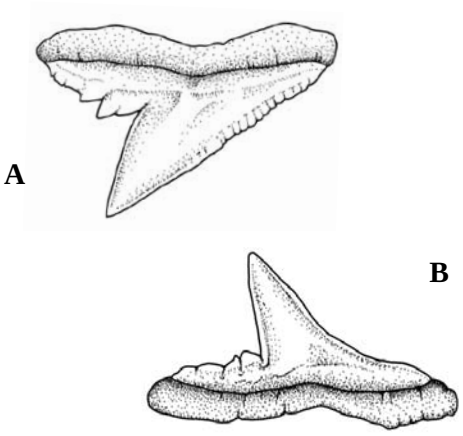

Figure 3. Upper anterior (A) and lower anterior (B) teeth of *Carcharhinus borneensis*. Illustrations by Lindsay Marshall.

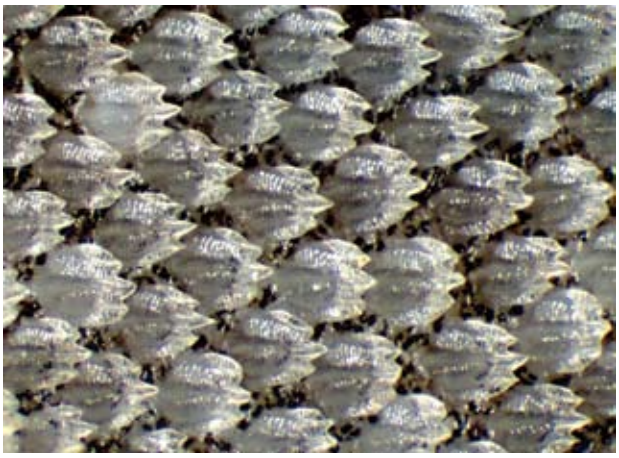

Figure 4. Cusps of the flank denticles of *Carcharhinus borneensis* (CSIRO H 6212–01, adult male 576 mm TL).

with narrow and oblique cusps (except first tooth either side of symphysis); mesial edges nearly straight, distal edge deeply notched, both edges finely serrated; base of distal edge with several small cusplets which are also finely serrated; single symphysial tooth small and upright. Lower teeth with narrower cusps which are about as oblique as uppers; distal edge deeply notched, mesial edge concave, both edges either smooth (smallest specimens) or finely serrated (larger specimens); single symphysial tooth small, narrow and upright.

Lateral trunk denticles small, imbricate, suboval to subcircular, with 3 short, stout cusps; crowns usually slightly longer than wide, with 3 prominent longitudinal ridges (medial ridge slightly stronger and more pronounced) that extend entire length of crown onto cusps; medial cusp short but strong, shorter than rest of crown, flanked by a pair of slightly shorter lateral cusps.

Pectoral fins short and relatively narrow, weakly falcate; anterior margin slightly to moderately convex, apices narrowly rounded; posterior margin weakly concave; free rear tip moderately rounded to somewhat angular, inner margin weakly convex; base broad about 69 (54–62)% of fin length; length from origin to rear tip 1.24 (1.17–1.32) times anterior margin length; similar in area to first dorsal fin; origin under third to under fourth gill slit; fin apex about opposite free rear tip when fin is elevated and adpressed to body.

Pelvic fins small, triangular and not falcate; length of anterior margin 0.38 (0.37–0.44) of pectoral-fin anterior margin; area about 1.5 times or less that of anal fin; anterior margin nearly straight and slightly concave near base; apex angular; posterior margin nearly straight or slightly concave; free rear tip bluntly rounded, inner margin nearly straight.

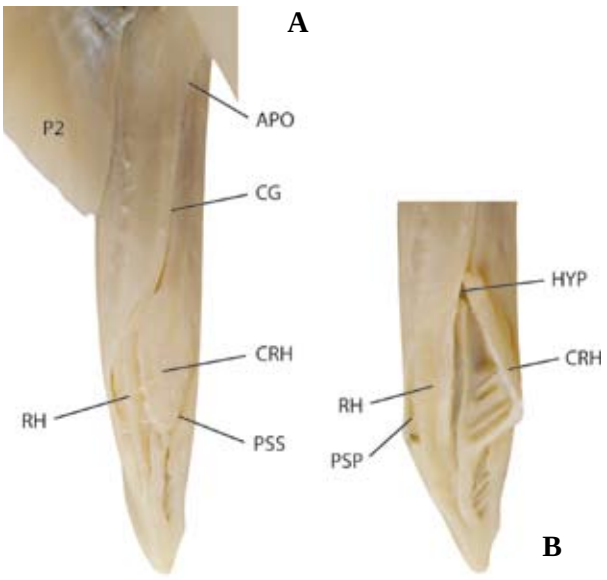

Figure 5. Clasper (left) of an adult male *Carcharhinus borneensis* (CSIRO H 6212–01, adult male 576 mm TL): A. glans not dilated; B. glans spread. APO, apopyle; CG, clasper groove; CRH, cover rhipidion; HYP, hypopyle; P2, pelvic fin; PSP, pseudopera; PSS, pseudosiphon; RH, rhipidion.

Claspers of adult male specimens moderately long, relatively narrow, somewhat stout, tapering sharply distally, outer length 6.2–6.5% TL, base width 18.5–21.1% of outer length; clasper glans extending to almost half of clasper outer length.

First dorsal fin relatively large, long-based, apically narrow and triangular, not falcate; anterior margin weakly convex (weakly concave basally); apex narrowly rounded; posterior margin distally straight and basally moderately concave; free rear tip very acutely pointed, inner margin concave to almost straight; origin opposite pectoral-fin mid-inner margin length, midpoint of base 1.2 (1.4–1.8) times closer to pectoral insertions than pelvic origins; free rear tip about opposite pelvic-fin origins; posterior margin arcing very slightly posteroventrally from apex, then abruptly so near free tip; insertion just posterior to dorsal-fin apex. First dorsal fin base 2.41 (1.64–2.12) in interdorsal space, 2.80 (2.05–2.50) in dorsal caudal margin; height 1.21 (1.24–1.80) in base; inner margin 1.67 (1.42–1.99) in height, 2.02 (1.92–2.85) in base.

Second dorsal fin very low, subtriangular; height 0.21 (0.22–0.29) times first dorsal-fin height, base 0.50 (0.38–0.51) times first dorsal-fin base; anterior margin nearly straight to very weakly convex; apex subangular; posterior margin weakly concave; free rear tip very long, acutely pointed, inner margin nearly straight; origin about opposite or just anterior to anal-fin midbase; rear tip well behind anal-fin free rear tip, in front of upper caudal-fin origin by 1.11 (0.52–0.93) times its inner margin; posterior margin curving strongly posteroventrally from apex; insertion opposite to slightly behind fin apex. Second dorsal fin base 1.66 (1.30–1.78) in dorsal–caudal space; height 2.83 (2.03–3.08) in base; inner margin 2.22 (1.92–2.56) times height, 1.27 (0.97–1.24) in base.

Anal fin apically narrow and strongly falcate; slightly larger than second dorsal fin; height 1.61 (1.08–1.52) times second dorsal-fin height, base length 1.22 (1.07–1.48) times second dorsal-fin base; anterior margin indented basally and distally broadly convex; apex narrowly to acutely pointed; posterior margin deeply notched at less than a right angle; free rear tip acutely pointed, inner margin nearly straight; origin well anterior to second dorsal-fin origin; insertion about level with second dorsal-fin midbase, anterior to fin apex; free rear tip in front of lower caudal-fin origin by a length subequal to its inner margin length; posterior margin slanting anterodorsally and then abruptly posterodorsally. Anal-fin base expanded anteriorly as very short preanal ridges (obscure), less than a quarter length of rest of base. Anal-fin base 1.49 (1.19–1.61) in anal–caudal space; height 2.15 (1.63–2.60) in base; inner margin 1.21 (1.22–1.77) times height, 1.77 (1.15–1.65) in base.

Caudal fin narrow-lobed and asymmetrical, with short terminal lobe and prominent, long, narrowly expanded, non-falcate ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave just anterior to subterminal notch, with prominent lateral undulations; preventral margin weakly convex, tip of ventral caudal-fin lobe bluntly pointed to moderately rounded; lower postventral margin nearly straight; upper postventral margin nearly straight except for convex section at subterminal notch; subterminal notch a narrow, deep slot; subterminal margin nearly straight, terminal margin irregular and moderately concave, lobe formed by these margins angular, tip of tail narrowly rounded. Length of dorsal caudal margin 3.04 (2.62–2.98) in precaudal length, preventral caudal margin 2.73 (2.24–2.58) in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 3.71 (2.83–3.11) in dorsal caudal margin, subterminal margin length 1.76 (1.17–1.81) in terminal margin.

Vertebral counts listed in Table 2. Counts of total vertebral centra (TC) 114+ (117–121, n=6), precaudal centra (PC) 62 (57–63, n=6), monospondylous precaudal (MP) centra (33–36, n=3), diplospondylous precaudal (DP) centra (21–26, n=3), diplospondylous caudal (DC) centra 52+ (56–60, n=6); MP centra (28.0–30.8)%, DP centra (17.9–22.0)%, and DC centra 48.3 (47.5–51.3)% of TC centra. Ratios of DP/MP centra (0.58–0.79), DC/MP centra (1.67–1.79).

COLORATION.— When fresh and in preservative: dorsal surface of head, trunk and tail slate-grey (preserved specimens often dark slate-grey), graduating to white ventrally on midlateral surface. Demarcation of

Table 2. Vertebral counts and ratios for the holotype (RMNH 7386), three old specimens and three recently collected specimens of *Carcharhinus borneensis*. Ranges for all specimens are also provided. Asterix (*) refers to vertebral counts obtained from Garrick (1982).

	RMNH 7386 *	RMNH 7666 *	BMNH 1895.2.28 *	SU 66750 *	CSIRO H 6212–01	CSIRO H 6226–01	CSIRO H 6226–02	**Min.**	**Max.**
Vertebrae:									
MP					33	34	36	33	36
DP					26	25	21	21	26
DC	52+	57	56	58	59	59	60	56	60
PC	62	61	62	63	59	59	57	57	63
TC	114+	118	118	121	118	118	117	117	121
%MP					28.0	28.8	30.8	28.0	30.8
%DP					22.0	21.2	17.9	17.9	22.0
%DC		48.3	47.5	47.9	50.0	50.0	51.3	47.5	51.3
%PC		51.7	52.5	52.1	50.0	50.0	48.7	48.7	52.5
DP/MP					0.79	0.74	0.58	0.58	0.79
DC/MP					1.79	1.74	1.67	1.67	1.79

light and dark surfaces (waterline) of head strong (light ventral colour just visible in dorsoventral view of head), extending along lateral angle of the snout anteriorly to level of nostrils, extending dorsoposteriorly to just above upper margin of eye; then after posterior eye extending gradually ventroposteriorly to upper edge of first gill slit; gill slit membranes entirely whitish; a narrow dusky area extending around ventral margin of eye, just visible ventrally. Waterline somewhat diffuse above pectoral fins but usually with a distinct pale area above pectoral-fin base; extending somewhat diffusely along abdomen almost to origin of pelvic fin; pale area extending almost as a pale stripe midlaterally on trunk below posterior half of first dorsal fin; waterline directed posterodorsally below first dorsal-fin insertion, well demarcated, extending along tail mid-laterally anteriorly and extending above midlateral region on caudal peduncle; pale area continuing onto base of caudal fin, apparent as a pale marking along the upper lobe to the origin of the terminal lobe. Some specimens with an irregular row of diffuse-edged, whitish spots or blotches along body and occasionally head, usually only present on one side of body (possibly artificial); one specimen (IPPS 47-07) with a very distinctive row of small white blotches extending from beneath midbase of first dorsal fin to about level of second dorsal-fin origin in a weakly convex line, a second row extending just below base of first dorsal fin on left side, around its origin and extending only slightly posteriorly of origin on right side, and some whitish markings on dorsal head (Fig. 6). First dorsal fin slate grey, distal third dusky, lower two-thirds of posterior margin with a broad whitish marginal band extending onto free rear tip. Second dorsal fin slate grey, anterior margin narrowly dark-edged, posterior margin whitish, free rear tip mostly pale. Anal fin mostly pale. Caudal fin dusky, paler medially; anterior margin narrowly black-edged; terminal lobe with broad dark greyish marking; similar dark marking extending along upper postventral margin caudal fork; lower postventral margin and preventral margins whitish. Pectoral fins not uniform on both surfaces; upper surface mostly slate grey (sometimes darker distally), with a broad whitish posterior margin; origin whitish; ventral surface mostly white, usually with a broad, variably developed dusky patch (sometimes dark grey) distally. Pelvic fins whitish on both surfaces. Claspers whitish. Eyes silvery yellow with a black pupil; nictitating membrane whitish.

SIZE.— Specimens retained range in length from 237–618 mm TL. Two specimens collected in the 1800s had fresh umbilical scars at 237 and 274 mm, indicating that the size at birth is close to these sizes; four specimens of 341–373 mm had well healed, but still obvious umbilical scars. Five males (three retained, two not retained) with lengths of 548–576 mm were mature. Additional material collected by one of the authors (AL) included mature males with lengths of 590–620 mm and several pregnant females with lengths of 610–650 mm. Litter size of the pregnant females was 6.

DISTRIBUTION.— The first two specimens of this

Figure 6. Dorsal anterior view of *Carcharhinus borneensis* (IPPS 47/07, immature male 373 mm TL) illustrating the inconsistent and irregular rows of white spots and blotches.

species were collected in the 1800s from northwestern Kalimantan. Although reported from the Philippines and Java, these records cannot be validated. This species was not found in either of these regions during recent surveys of the area (Compagno *et al*., 2005b; White *et al*., 2006). A single specimen was collected from China in 1936 (SU 66750), but this species has not been reported from China since then. During recent surveys around the whole island of Borneo, the only locality *C. borneensis* was recorded from was Mukah in Sarawak (02°53′ N, 112°05′ E). Thus, although the range of this species was possibly more widespread in the 1800s, presently it has an extremely restricted range off northwestern Borneo.

DISCUSSION

Carcharhinus borneensis is considered to be one of the rarest, most poorly known carcharhinid sharks, previously only known from five valid specimens, all juveniles. This paper provides a detailed redescription of this species based on the holotype and 12 other specimens, including recently collected adults, from Borneo and provides images and a colour description of fresh specimens for the first time.

Carcharhinus borneensis is a small carcharhinid species which was placed into the 'porosus' group by Compagno (1988). This group of sharks are characterised by their elongate and narrowly rounded snouts and their upper teeth which have narrow, oblique cusps with deeply notched postlateral edges and strong cusplets (Compagno, 1988). *Carcharhinus borneensis* differs from most of its congeners in having the second dorsal-fin origin well behind the anal-fin origin and about opposite the anal-fin midbase. It shares this characteristic with *C. macloti*, *C. porosus* and *C.* sp. A [*sensu* Compagno *et al*., 2005a]. It differs from *C. macloti* in having a much shorter first dorsal-fin inner margin (35–52% vs. about 67% of first dorsal-fin base), rostrum not hypercalcified (vs. obviously hypercalcified), and upper anterior teeth with fine serrations (vs. no serrations). It differs from *C. porosus* and *C*. sp. A in having a row of enlarged hyomandibular pores alongside the mouth corners (vs. no enlarged hyomandibular pores), a lower second dorsal fin (its height 1.9–2.6 in its inner margin vs. 1.5–1.9), and less teeth (11–12/11–12 vs. 13–15/12–15).

Carcharhinus borneensis is similar morphologically to *Rhizoprionodon* species, which is highlighted in the misidentification in Yano *et al*. (2005) where *R. acutus* specimens were confused with *C. borneensis* in their treatment of the latter species. Although similar to *Rhizoprionodon* species, *C. borneensis* is clearly separable in having a more anteriorly placed second dorsal fin, second dorsal fin only slightly smaller than anal fin and origin opposite its midbase (vs. origin opposite anal-fin insertion), anal-fin posterior margin deeply notched (vs. nearly straight), and pre-anal ridges barely noticeable (vs. long and prominent, about length of anal-fin base). Compagno (1988) also states that the cranial anatomy of *C. borneensis* is closer to its congeners rather than to species of *Rhizoprionodon*.

The juveniles and 'adults' of *C. borneensis* were typically very similar morphologically, however, a number of differences were still recorded. The larger specimens (574–618 mm TL, n=7) differed slightly from the juvenile specimens (237–373 mm TL, n=6) in the following characteristics: head shorter (head length

22.3–23.8 vs. 24.2–26.5% TL, prebranchial length 18.4–19.6 vs. 20.2–20.8% TL), preorbital snout slightly shorter (8.6–9.6 vs. 9.5–10.2% TL), dorsal fins slightly further apart (interdorsal space 21.4–22.7 vs. 20.7–21.6% TL), eyes slightly smaller (length 1.6–1.8 vs. 1.9–2.5% TL), and head slightly narrower (interorbital space 8.9–9.4 vs. 9.5–10.5% TL). Females and males were almost morphologically identical, but the adult males (574–576 mm TL, n=3) had more anteriorly positioned pelvic fins compared to the females (578–618 mm TL, n=4). This is reflected in the following measurements: pectoral–pelvic space 18.9–20.1% TL in males vs. 20.5–20.8% TL in females, and mid-base of first dorsal fin to pelvic fin origin 10.5–11.1 vs. 11.4–12.9% TL.

Despite the wide coverage of survey sites around Borneo in recent surveys of the chondrichthyan fauna of this region, specimens of *C. borneensis* were only collected at Mukah in Sarawak. Although this species had not been recorded since 1937, it appears to be in substantial numbers near this one location, but was not recorded anywhere else in Borneo. The original specimens of this species were collected from northwestern Kalimantan, near Pontianak which is a heavily fished area. This species may have been severely depleted in these areas and it is possible that it is now restricted to the area around Mukah. More surveys of fish landing sites in western Borneo are needed to confirm this. Given that this species is currently listed as Endangered by the IUCN and still little is known of its actual range, other than probably being very restricted, more research is required to determine the conservation status of this species in light of this new information. Actions to arrest population declines throughout its remaining range should be developed to ensure it is not further depleted. Re-assessment of the IUCN conservation status of this species should also be undertaken to include this new information.

ACKNOWLEDGEMENTS

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Glyphis fowlerae sp. nov., a new species of river shark (Carcharhiniformes; Carcharhinidae) from northeastern Borneo

Leonard J.V. Compagno[1], William T. White[2] & Rachel D. Cavanagh[3]

[1] formerly Shark Research Center, Iziko – Museums of Cape Town, Cape Town 8000, SOUTH AFRICA
[2] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[3] British Antarctic Survey, Cambridge, High Cross, Madingley Road, CB3 0ET, UNITED KINGDOM

ABSTRACT.— A new river shark, *Glyphis fowlerae* sp. nov., is described from 14 type specimens from Malaysian Borneo, including 13 specimens collected in freshwater from the vicinity of Kampung Abai in the lower reaches of the Kinabatangan River, Sabah. *Glyphis fowlerae* differs from other members of the genus by a combination of vertebral counts, dentition, coloration and morphology, particularly in the comparative heights of the dorsal fins. A second, rarely collected species of *Glyphis* from Sarawak (Malaysian Borneo) is also compared (based on colour images) to the new species and its status discussed. One of the syntypes of *Glyphis gangeticus*, described from India, is designated as a lectotype for that species.

Key words: Carcharhinidae – *Glyphis fowlerae* – new species – Borneo – freshwater

PDF contact: william.white@csiro.au

INTRODUCTION

The genus *Glyphis* was proposed by Agassiz (1843) for a living species of carcharhinid shark (Family Carcharhinidae), *Carcharias* (*Prionodon*) *glyphis*, which had been described by Müller & Henle (1839) from a single stuffed specimen without locality but with distinctive spear-shaped (hastate) lower anterior teeth, small eyes and a large second dorsal fin. A detailed account of the nomenclatural history of *Glyphis* can be found in Compagno (1979, 1988, 2003). Although considered by many authors to be a synonym of the genus *Carcharhinus* Blainville, 1816, Compagno (1984) revived *Glyphis* as a genus for *C*. (*P*.) *glyphis* and *C*.(*P*.) *gangeticus*, and noted that there were additional species represented by specimens from Borneo, New Guinea and Queensland, Australia (Prof. J.A.F. Garrick pers. comm., to senior author). The vernacular name 'river sharks' was proposed by Compagno (1984) for *Glyphis* species because the Ganges Shark (*G. gangeticus*) and other species occur in tropical rivers and associated deltas in the Indo–West Pacific.

Compagno *et al*. (2008) provided a detailed description of a new species of *Glyphis* from northern Australia and New Guinea, *G. garricki* Compagno, White & Last, 2008, which had previously been referred to as *G*. sp. C [*sensu* Compagno & Niem, 1998; Compagno *et al*., 2005]. These authors also synonymised *G*. sp. A [*sensu* Last & Stevens, 1994; *sensu* Compagno & Niem, 1998] with *G. glyphis* (Müller & Henle, 1839) and provided a detailed redescription of this species. Compagno *et al*. (2008) recognised 5 species of *Glyphis*: *G. garricki* Compagno, White & Last, 2008; *G. gangeticus* (Müller & Henle, 1839); *G. glyphis* (Müller & Henle, 1839); *G. siamensis* (Steindachner, 1896); and an undescribed species from Borneo, *G*. sp. B [*sensu* Compagno & Niem, 1998].

The presence of *Glyphis* in Borneo was first reported by Compagno (1984), based on a specimen in a museum in Vienna (NMW), was tentatively identified as *G. glyphis*, but differences in vertebral counts and the need for further work were noted. In 1996, the Darwin Elasmobranch Biodiversity Conservation and Management project in Sabah was established in collaboration with the Department of Fisheries Sabah, the IUCN Species Survival Commission's Shark Specialist Group, WWF Malaysia and the Universiti Malaysia Sabah. During an elasmobranch survey of Sabah between January 1996 and July 1997, which included riverine and estuarine habitats, a number of *Glyphis* specimens were collected from the vicinity of Kampung Abai on the Kinabatangan River that were considered conspecific with the NMW specimen collected over a century ago (Manjaji, 2002a, b). Compagno & Niem (1998) provided a brief account of this species and provided the name Borneo River Shark *Glyphis* sp. B. In market surveys of greater Borneo funded by the National Science Foundation (NSF) over

the last decade, several additional specimens of *G*. sp. B were collected near the same locality on the Kinabatangan River. During the same surveys, two specimens of another species of *Glyphis* were collected from Mukah (Sarawak, Malaysian Borneo) that is not conspecific with *G*. sp. B and requires further investigation to determine its identity.

Yano *et al*. (2005) provided a description of the Kinabatangan River Shark, *Glyphis* sp. B (as *G*. sp.), based on one of the Darwin project specimens. Compagno *et al*. (2005) also provided an account of *G*. sp. B and a comparison of vertebral and tooth counts with other members of the genus. More recently, Fahmi & Adrim (2009) provided the first record of a species of *Glyphis* from Indonesian Borneo. This specimen, an adult male collected in 2005 from Sampit Bay in Central Kalimantan, was not retained due to its large size (1660 mm total length, TL). They noted its similarity and difference to *G*. sp. B in many morphological characters, but given the specimen was not retained, an accurate identification could not be made.

The present account provides a formal name and description of *Glyphis* sp. B based on a population from the Kinabatangan River, eastern Sabah. Comparisons with other members of this genus are also provided and a lectotype is designated for *Glyphis gangeticus*.

METHODS

Terminology for morphology follows Compagno (1973, 1979, 1988, 2001, 2003), Compagno & Springer (1971), Compagno *et al*. (2005) and Taylor *et al.* (1983). Measurement terminology is from Compagno (1984, 2001, 2003) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Dentitional terms are modified from Compagno (1970, 1979, 1988, 2001, 2003). The major differences as used here are the substitution of the orientation terms `distal' for `postlateral', `mesial' for `premedial', `labial' for `outer' and `lingual' for `inner', more in conformity with current European terminology. Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1970, 1979, 1988, 2003), including 'A' ratio (length of penultimate monospondylous precaudal centrum/length of first diplospondylous precaudal centrum x 100) and 'B' ratio (length/width of penultimate monospondylous precaudal centrum x 100).

The holotype and all 13 paratypes of *Glyphis fowlerae* were measured in full (Table 1). For comparison, the two *G. gangeticus* types and the holotype of *G. siamensis* were also measured (Table 1). Comparative measurements for *G. garricki* and *G. glyphis* from northern Australia are provided in Compagno *et al*. (2008). Meristics were taken from radiographs of the holotype, 12 of the paratypes and one other specimen of *Glyphis fowlerae*, and from the paralectotype (MNHN 1141) of *G. gangeticus* and the holotype (NMW 61397) of *G. siamensis*. Counts were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of upper lobe of caudal fin) and caudal (centra of the caudal fin) vertebrae (Table 2). Morphometric and meristic data for the holotype are followed in parentheses by the ranges of the paratypes in the descriptive section. Tooth row counts were taken *in situ*, from radiographs or from excised jaws. Teeth and denticles were examined after maceration with sodium hypochlorite (NaOCl).

Specimens, including types, are referred to by the following prefixes for their registration numbers: CSIRO, Australian National Fish Collection, Hobart, Australia; IPMB, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia; SMEC, Sabah Museum Elasmobranch Collection, Kota Kinabalu, Sabah, Malaysia; LWF, L.W. Filewood field numbers for specimens collected in Papua New Guinea; MNHN, Museum National d'Histoire Naturelle, Paris; NMW, Naturhistorisches Museum, Vienna; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; SAM, South African Museum, Cape Town, South Africa; QM, Queensland Museum, Brisbane, Australia; WAM, Western Australian Museum, Perth, Australia; ZMB, Zoologisches Museum, Humboldt Universitat, Berlin, Germany; ZSI, Zoological Survey of India, Calcutta, India. Field accession numbers for specimens collected on the NSF elasmobranch project (NSFEP) in Sarawak, Malaysian Borneo, which were photographed but retained specimens are missing, are prefixed with the letters BO (data and images for these specimens are available at http://tapeworms.uconn.edu).

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus *Glyphis* Agassiz, 1843

Type species. *Carcharias* (*Prionodon*) *glyphis* Müller & Henle, 1839, by absolute tautonymy.

SPECIES.— *Glyphis* includes five nominal species: *G. fowlerae* sp. nov.; *G. garricki* Compagno, White & Last, 2008; *G. gangeticus* (Müller & Henle, 1839); *G. glyphis* (Müller & Henle, 1839); *G. siamensis* (Steindachner, 1896); and possibly another, undescribed species from Borneo, *G.* sp.. *Carcharias murrayi* Günther, 1883 (from the delta of the Indus River, Pakistan) is a possible synonym of *G. gangeticus* or a distinct species, but the unique holotype, a stuffed specimen in the collection of the British Museum of Natural History, is missing, presumably lost (O. Crimmen, J. Macclaine, pers. comm.).

Glyphis fowlerae sp. nov.

Figs 1–4; Tables 1 and 2

Glyphis glyphis (Müller & Henle, 1839): Compagno, 1984: p 509, figs. Misidentification.
Glyphis sp. B: Compagno & Niem, 1998: pp 1318, 1360, fig. 25; Compagno *et al*., 2005: pp 309, 311, 312, figs, pl. 55.
Glyphis sp.: Yano *et al*., 2005: pp 248–250, pl. 160, 161.

Holotype. IPMB 38.14.02, female 577 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41′10.81″ N 118°23′08.35″ E, 30 Apr. 2003.
Paratypes. 13 specimens: CSIRO H 5784–01, juvenile male 517 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, Mar. 1999; IPMB 38.14.03, juvenile male 487 mm TL, collected with holotype; BMNH 1997.10.14.1, female 538 mm TL, SMEC 352, female 582 mm TL, SMEC 354, female 505 mm TL, SMEC 355, juvenile male 575 mm TL, SMEC 356, juvenile male 667 mm TL, SMEC 357, juvenile male 632 mm TL, SMEC 348 (currently housed in LJVC collection Cape Town), female 778 mm TL, SMEC 358 (currently housed in LJVC collection Cape Town), juvenile male 600 mm TL, SMEC 359 (currently housed in LJVC collection Cape Town), juvenile male 606 mm TL, SMEC 353 (location uncertain), female 566 mm TL Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41′10.19″ N 118°23′02.21″ E, 1997; NMW 61401, female 627 mm TL, Borneo, no further locality data.
Other material. 1 specimen: CSIRO H 7089–01, juvenile male 473 mm TL, Kampung Abai, Kinabatangan River, Sabah, Malaysia, 05°41′ N, 118°23′ E.

DIAGNOSIS.— A species of *Glyphis* with the following combination of characters: snout short, broadly rounded in dorsoventral view; minimum distance from mouth to nostril 1.1–1.6 times nostril width; lips usually concealing teeth when mouth closed; lower teeth with erect, narrow, moderately hooked to straight cusps, with notched mesial and distal edges, and low mesial and distal shoulders or blades (except in posterior teeth); anteroposterior tooth row counts 13–15/13–15; total tooth row counts 28–31/29–32 or 60–63; interdorsal space 17.0–19.5% TL; anterior margin of pectoral fin slightly convex, pectoral length 11.6–13.4% TL; length of pelvic-fin anterior margin 6.3–7.7% TL, 36–40% of length of pectoral-fin anterior margin; pelvic-fin height 4.6–6.3% TL; first dorsal fin not falcate, with concave posterior margin, free rear tip just anterior to pelvic-fin origins, its length 16.9–19.1% TL; second dorsal-fin length 10.5–12.3% TL, anterior margin length 7.5–9.7% TL, its base length 7.4–9.3% TL and 1.4–1.9 times second dorsal-fin height, its height 4.7–6.0% TL and 58–68% of first dorsal height; anal-fin height 4.1–5.0% TL and 74–102% of second dorsal-fin height, its base 65–94% of second dorsal-fin base; caudal-fin subterminal margin weakly concave; total vertebral count 196–209; monospondylous precaudal count 60–67, 30–33% of total count; diplospondylous precaudal count 43–52, 22–26% of total count; diplospondylous caudal count 82–96, 42–46% of total count; precaudal count 108–114, 54–58% of total count; boundary coloration (watermark) on head diffuse, extending through lower level of eye; in young, watermark well defined, diffuse along trunk, situated near lateral midline; dorsal, pectoral, pelvic and anal fins plain; ventral caudal-fin lobe, and postventral and dorsal margins, dusky to blackish.

DESCRIPTION.— Body stout, trunk subcircular and almost pear-shaped in section at first dorsal-fin base, length of trunk from fifth gill slits to vent 1.10 (1.01–1.12) times head length. Predorsal, interdorsal and postdorsal ridges absent from midline of back, lateral ridges absent from body. Caudal peduncle stout, rounded-hexagonal in section at second dorsal-fin insertion, postdorsal and postventral spaces flattened and often with a shallow median groove anteriorly, lateral surfaces subangular and with a broad, very low, inconspicuous lateral ridge on each side at middle of the peduncle that extends anteriorly to the pelvic-fin midbases and posteriorly onto the caudal-fin base; height of caudal peduncle at second dorsal-fin insertion 1.03 (1.11–1.36) times its width, 1.58 (1.21–1.63) times in dorsal–caudal space. Precaudal pits present; upper pit a pronounced, subtriangular depression, not arcuate and crescentic; lower pit rudimentary, essentially a dimple at the lower caudal-fin origin.

Head length to fifth gill opening 0.84 (0.74–0.82) times in pectoral–pelvic space. Head broad and somewhat flattened, ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, nearly straight on snout, convex above eye, concave at nape and convex above gills and progressively elevated towards first dorsal fin; slightly convex ventrally along lower jaws and beneath gills. In dorsoventral view, head anteriorly rounded and U-shaped, with gill septa expanded outwards. Snout short, preoral snout length 0.80 (0.70–0.83) times mouth width; tip broadly rounded in dorsoventral view and with a slight angle at nostrils but not noticeably indented anterior to nostrils; snout narrowly rounded in lateral view, slightly convex above and below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, with height 1.01 (0.79–1.23) in eye length. Eyes small, length 19.79 (18.13–26.27) times in head length; situated lateral on head; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

Spiracles absent. First three gill slits subequal in height, first opening usually much larger, fifth smallest; fifth slit about 0.85 (0.60–0.88) times height of third; height of third about 9.07 (6.95–8.93) in head length, 2.18 (2.03–3.58) times eye length. Margins of first four gill slits nearly straight, posterior margin irregular; fifth slightly

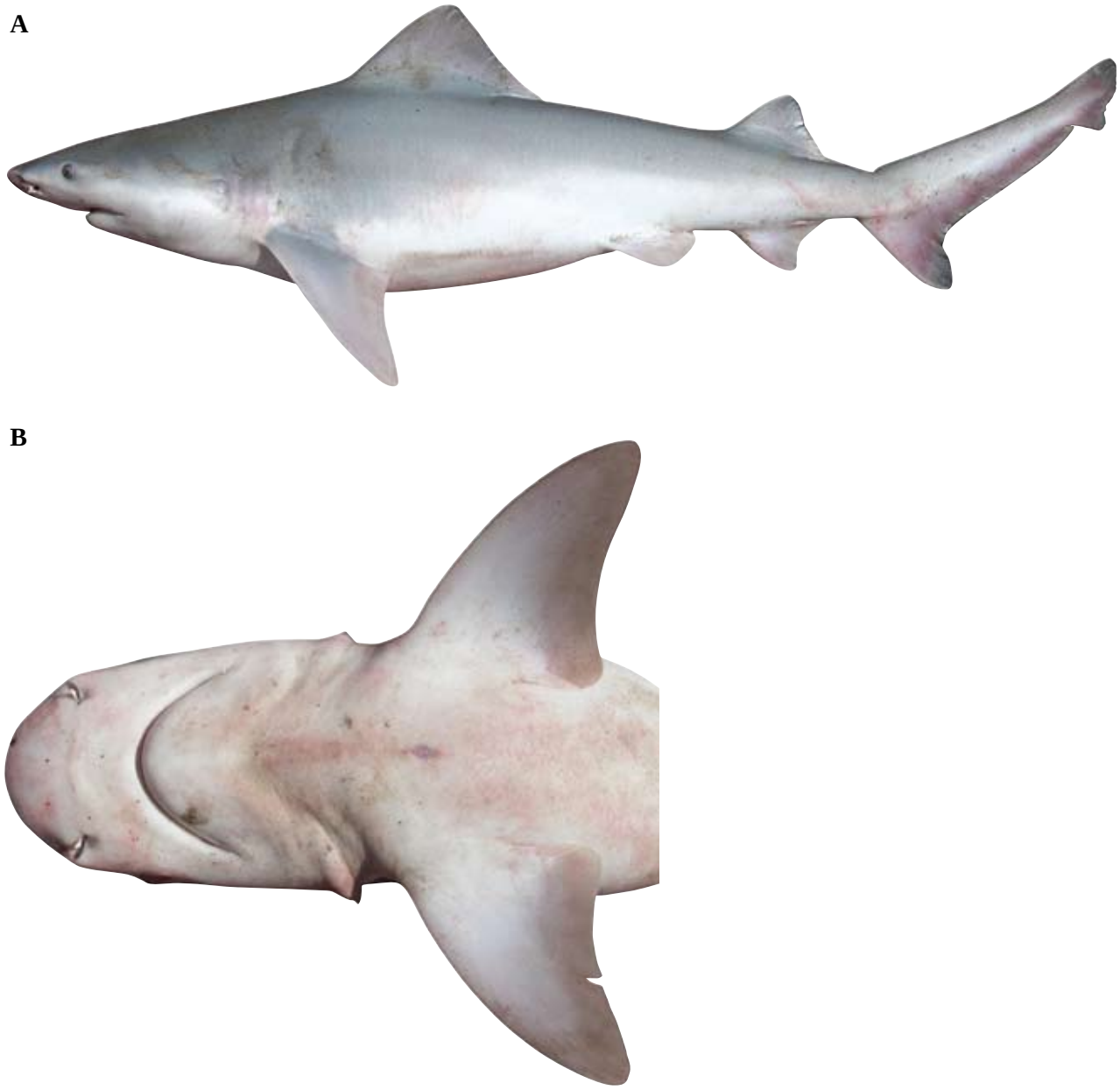

Figure 1. Juvenile female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh): A. lateral view; B. anterior ventral view.

concave; upper edges of gill slits 2–4 most elevated; upper end of highest gill about level with upper edge of eye. Gill filaments not visible from outside. Gill-raker papillae absent from gill arches.

Nostrils with large, oval incurrent apertures; prominent triangular anterior nasal flaps with bluntly pointed tips, mesonarial flaps absent, small subcircular excurrent apertures, posterior nasal flaps vestigial or absent; well in front of mouth; width 4.04 (3.21–3.95) in internarial width, 0.70 (0.45–0.73) in eye length, 1.52 (1.31–1.86) in longest gill-opening.

Mouth broadly parabolic and large; width 2.67 (2.36–2.76) in head length; mouth length 1.71 (1.76–1.98) in mouth width. Lips usually concealing teeth when mouth is closed. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve narrow, width slightly less than eye diameter, papillose. No large buccal papillae on floor or roof of mouth behind maxillary valve. Palate, floor of mouth and gill arches covered with buccopharyngeal denticles. Labial furrows short, uppers 1.08 (0.37–1.52) times as long as lowers, lowers concealed by overlapping upper lip; anterior ends of uppers far behind eyes. Labial cartilages appear to be absent.

Table 1. Proportional dimensions as percentages of total length for the holotype (IPMB 38.14.02) and ranges for the 13 paratypes of *Glyphis fowlerae* sp. nov. Measurements of the lectotype and paralectotype of *G. gangeticus* and the holotype of *G. siamensis* are also provided.

	G. fowlerae sp. nov.			*G. gangeticus*		*G. siamensis*
				Lect.	Paralect.	Holotype
	Holotype	Paratypes (n=13)		ZMB	MNHN	NMW
		Min.	Max.	4474	1141	61397
TL	577	487	778	1850	556	630
PCL	74.8	73.5	75.8	75.8	73.6	73.0
PRN	4.8	4.8	5.3	3.6	4.6	3.8
POR	7.7	7.5	8.3	6.5	6.6	7.3
POB	8.3	8.3	10.5	7.0	7.7	7.8
PGI	21.3	20.4	22.1	17.3	19.5	19.7
HDL	25.7	24.5	26.0	24.1	24.6	24.3
PP1	24.3	21.6	24.1	21.1	22.2	23.0
PP2	51.5	48.7	50.5	49.8	48.0	50.0
SVL	53.9	52.0	53.6	54.3	50.9	–
PAL	61.0	59.1	62.1	64.6	59.4	–
PD1	28.6	28.0	30.5	28.9	28.8	28.6
PD2	61.4	58.5	62.0	61.6	60.8	61.4
IDS	18.3	17.0	19.5	20.4	19.0	19.2
DCS	6.9	6.4	7.1	7.0	6.3	6.8
PPS	21.5	18.9	21.0	21.7	18.8	–
PAS	5.9	4.7	5.9	9.0	5.8	–
ACS	5.7	5.0	6.1	6.4	5.7	–
EYL	1.3	0.9	1.4	0.8	1.3	0.7
EYH	1.3	1.0	1.4	0.8	1.4	–
INO	12.1	11.5	12.7	10.4	10.9	–
NOW	1.9	1.9	2.3	1.1	1.9	1.4
INW	7.5	7.0	7.7	8.8	6.7	7.3
ANF	0.6	0.3	0.8	0.0	0.6	0.5
MOL	5.6	4.9	5.7	3.8	6.2	5.9
MOW	9.6	9.4	10.7	10.3	9.3	9.5
ULA	0.4	0.3	0.6	0.0	0.6	0.5
LLA	0.4	0.2	0.9	0.0	0.5	–
GS1	2.9	2.9	3.8	3.6	3.5	2.7
GS2	2.9	2.9	3.8	3.6	3.7	–
GS3	2.8	2.9	3.6	3.5	3.7	–
GS4	2.7	2.5	3.4	3.4	3.2	–
GS5	2.4	2.0	2.9	–	3.5	–
HDH	11.0	11.8	17.8	–	11.5	–
HDW	12.8	12.3	17.2	–	11.5	11.9
TRH	11.1	12.2	14.9	11.9	10.8	13.0
TRW	11.9	11.0	15.3	–	9.4	–
CPH	4.4	4.2	5.7	4.0	4.3	4.0
CPW	4.2	3.1	4.7	–	2.3	–
P1L	12.0	11.6	13.4	11.4	11.5	–
P1A	17.1	16.7	20.0	20.0	19.9	18.3
P1B	7.1	6.9	8.5	7.3	6.9	–

Table 1. cont'd.

	G. fowlerae sp. nov.			*G. gangeticus*		*G. siamensis*
				Lect.	Paralect.	Holotype
	Holotype	Paratypes (n=13)		ZMB	MNHN	NMW
		Min.	Max.	4474	1141	61397
P1H	15.0	12.1	17.9	18.6	16.9	–
P1I	4.8	4.1	6.1	4.4	6.3	–
P1P	14.0	12.8	15.0	18.4	17.2	–
P2L	8.9	8.8	10.3	7.8	8.9	7.0
P2A	6.3	6.3	7.7	5.6	7.3	–
P2B	5.9	5.5	6.8	6.2	5.8	–
P2H	6.3	4.6	6.3	4.5	6.1	–
P2I	3.0	2.6	3.7	2.4	3.3	–
P2P	6.6	5.9	7.7	6.0	6.6	–
CLO	–	1.6	2.2	6.4	1.4	–
CLI	–	4.0	4.7	8.6	4.5	–
CLB	–	0.7	0.8	1.2	0.5	–
D1L	18.2	16.9	19.1	15.5	17.0	17.3
D1A	13.2	11.7	14.6	13.2	14.4	–
D1B	14.2	12.6	14.7	12.4	12.0	12.4
D1H	7.8	7.6	10.2	8.6	9.9	–
D1I	4.5	3.8	4.8	2.9	5.0	4.3
D1P	10.2	9.4	12.9	11.0	10.7	–
D2L	10.5	11.0	12.3	11.9	10.6	10.6
D2A	7.5	8.0	9.7	7.0	7.8	–
D2B	7.4	7.8	9.3	7.7	7.1	6.7
D2H	5.1	4.7	6.0	4.3	4.6	–
D2I	3.5	2.9	4.0	2.7	3.4	3.3
D2P	6.2	5.6	7.5	6.5	6.4	–
ANL	10.2	8.7	11.5	7.6	10.0	–
ANA	8.4	7.4	9.3	5.8	8.8	–
ANB	7.0	5.8	7.9	5.2	6.9	–
ANH	4.7	4.1	5.0	3.6	4.4	–
ANI	3.4	3.0	3.7	2.2	3.4	–
ANP	5.3	4.3	5.3	4.3	5.0	–
CDM	25.5	24.7	26.5	24.3	27.1	27.0
CPV	10.8	11.0	12.3	11.1	11.6	–
CPL	4.7	4.4	5.5	6.2	5.9	–
CPU	14.3	12.8	14.7	13.5	13.4	–
CST	3.6	2.2	4.1	2.7	3.2	2.9
CTR	6.4	5.2	6.5	6.5	6.7	4.4
CTL	7.6	6.0	8.0	6.5	7.7	6.8
CFL	8.2	8.5	9.4	6.9	8.2	–
DPI	4.9	4.0	5.9	–	6.3	–
DPO	17.1	12.7	15.8	–	11.9	–
PDI	12.5	8.8	12.3	–	9.2	–
PDO	5.5	5.8	7.7	–	9.4	–
DAO	1.7	1.0	2.6	–	0.5	–
DAI	0.4	0.2	0.8	–	0.7	–

Figure 2. Lateral head view of juvenile female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh).

Teeth relatively few, in 28–31/29–32 rows or 60–63 total rows (both jaws), 1–2/2–3 series functional (n=5); not arranged in diagonal files, no toothless spaces at symphysis; highly differentiated in upper and lower jaws and along jaws; tooth row groups include upper and lower medials (M), anteriorised lower symphysials (AS), and anteriors (A), laterals (L), and posteriors (P) in both jaws. Tooth formula (n=5): upper jaw 4–5(P) 9–10(L) 1(A) + 1(M) + 1(A) 9–10(L) 3–4(P); lower jaw 4–5(P) 7–8(L) 2(A) + 1(S) 1(M) 1(S) + 2(A) 7–8(L) 4–5(P); or upper jaw 14–15 + 1 + 13–15, lower jaw 13–15 + 3 + 13–15. Lower teeth erect, narrow, with moderately hooked to straight cusps; mesial and distal edges notched; mesial and distal shoulders or blades low (except in posterior teeth). Upper teeth broader, flatter, more triangular, more bladelike than lowers; usually with broader, erect to semi-oblique straight cusps (except posteriors), coarser serrations (except for most posteriors); mesial edges un-notched; roots slightly arched. Upper medial teeth relatively high-crowned, very small; with a broad, triangular hooked cusp; a few coarse serrations on each side. The single row of upper anteriors have erect straight broad triangular cusps and are over three times as high as the medials and smaller and somewhat narrower than the adjacent laterals; these are compressed, bladelike teeth with straight edges and coarse serrations. Upper laterals begin as erect triangular flat, coarsely serrated bladelike teeth with broader bases than the anteriors and nearly straight or slightly concave mesial and distal edges; the second lateral being the largest upper tooth; the laterals gradually decrease in size from the second, with the cusp becoming more oblique, the mesial edge more convex, and the distal edge more concave until at the 9th or 10th tooth they make a transition to the carinate posteriors. Upper posteriors are low-crowned keel-like teeth with cusps weak or absent, a broad convex edge, and with serrations absent from most rows.

Lower medials are moderately large, erect and hooked-cusped, narrow symmetrical teeth with arched roots, finely serrated semihastate cusps, and crown feet developed as smooth shoulders without a blade and cutting edge. Lower symphysials larger and more robust than medials, and similar to adjacent anteriors except for being slightly smaller, with erect, moderately hooked, serrated non-hastate cusps, small mesial and distal blades, and deeply arched roots. Lower anteriors larger than symphysials but otherwise similar. Lower laterals with considerable variation along the dental band but with lower crowns, flatter cusps and relatively broader less arched roots than anteriors, large to small narrow-cusped teeth with shallowly notched mesial and distal edges and erect or semierect narrow, serrated cusps and blades. Lateral teeth decrease in size distally, with cusps becoming considerably lower and slightly more oblique. Lower posteriors similar to uppers, without cusps or cusplets and with convex broad edges, but smaller and lower-crowned than uppers. All teeth with transverse grooves and prominent centrolingual foramen on linguobasal attachment surface of roots. Tooth histological type orthodont, with a definite pulp cavity, crown formed of orthodentine and enameloid, and osteodentine confined to roots.

Lateral trunk denticles with flat, rhomboidal crowns about as wide as long, covered with faint reticulated depressions. Crown with 3 prominent longitudinal ridges that extend its entire length onto the cusps; medial cusp short but strong, shorter than the rest of crown; a pair of much shorter lateral cusps present. Denticle crowns widely spaced, not closely imbricated, with skin clearly visible between them. Denticle pedicels short and thick, but elevated crowns well above skin; denticle roots with 4 lobes.

Pectoral fins large, fairly narrow, weakly falcate; anterior margin moderately convex, apices narrowly rounded; posterior margin undulated, distal half convex, mesial half shallowly and broadly concave; free rear tip broadly rounded, inner margin moderately convex; base broad about 60% of fin length; length from origin to rear tip 1.43 (1.30–1.55) in anterior margin length; greater in area than first dorsal fin; origin varying from about under 2nd or 3rd gill slits; fin apex about opposite inner margin when fin is elevated and adpressed to body.

Pelvic fins triangular and not falcate; length of anterior margins 0.37 (0.36–0.40) of pectoral–fin anterior margins; area slightly larger than that of anal fin; anterior margin nearly straight; apices rounded; posterior margin nearly straight to weakly convex distally; free rear tip bluntly rounded, inner margin nearly straight; posterior margin, rear tip and inner margin forming a broadly triangular apex. Claspers of adult males not examined; those of immature males small, undifferentiated.

First dorsal fin apically narrow (apically angular in CSIRO H 5784–01) and broadly triangular, not falcate; angle of apex about 80–90°; anterior margin shallowly

concave basally and distally slightly convex; apex narrowly rounded to subangular; posterior margin distally straight and basally shallowly concave; free rear tip bluntly pointed, inner margin slightly concave; origin about opposite pectoral-fin insertion, midpoint of base 3.5 (2.4–3.8) times closer to pectoral insertions than pelvic origins; free rear tip just anterior to pelvic-fin origins; posterior margin arcing posteroventrally from apex; insertion well behind level of dorsal-fin apex. First dorsal-fin base 1.28 (1.20–1.51) in interdorsal space, 1.79 (1.71–2.09) in dorsal caudal margin; height 1.82 (1.23–1.83) in base length; inner margin 1.74 (1.74–2.32) in height, 3.17 (2.63–3.84) in base length.

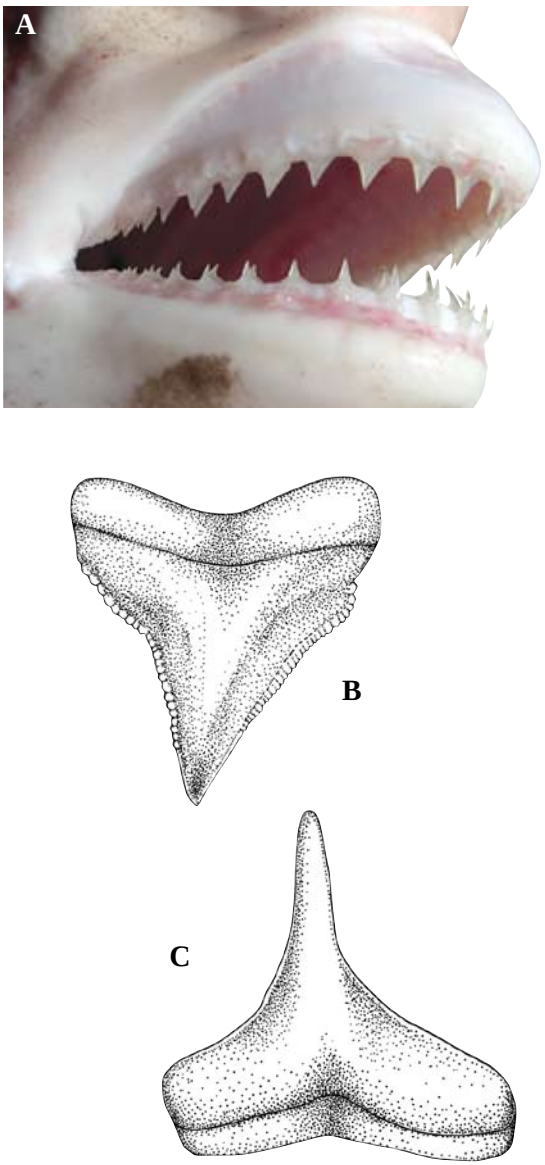

Figure 3. Teeth of the female holotype of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, 577 mm TL, fresh): A. jaw when fresh; B. upper mesial tooth; C. lower mesial tooth. Illustrations by Lindsay Marshall.

Figure 4. Flank denticles of *Glyphis fowlerae* sp. nov. (IPMB 38.14.02, holotype, juvenile female 577 mm TL).

Second dorsal fin apically narrow (moderately rounded in CSIRO H 5784–01), broadly triangular, very weakly falcate; height 0.65 (0.58–0.69) times first dorsal-fin height, base 0.52 (0.58–0.69) times first dorsal-fin base; anterior margin concave basally, becoming weakly convex distally; apex moderately rounded; posterior margin distally convex and then slightly concave; free rear tip acutely pointed, inner margin nearly straight; origin well behind pelvic-fin insertions and about opposite or slightly behind pelvic-fin free rear tips; rear tip about opposite anal-fin free rear tip, in front of upper caudal-fin origin by 0.53 (0.32–0.76) times its inner margin length; posterior margin curving posteroventrally from apex; insertion slightly behind fin apex. Second dorsal-fin base 0.93 (0.74–0.90) in dorsal–caudal space; height 1.45 (1.32–1.92) in base; inner margin 1.44 (1.32–1.68) in height, 2.09 (2.23–3.00) in base.

Anal fin apically narrow and falcate; height 0.93 (0.74–1.02) times second dorsal-fin height, base length 0.94 (0.65–0.93) times second dorsal-fin base; anterior margin concave basally and distally convex; apex bluntly pointed or narrowly rounded; posterior margin broadly notched at slightly more than a right angle; free rear tip acutely pointed, inner margin nearly straight to slightly concave; origin slightly behind second dorsal-fin origin; insertion opposite or slightly behind second dorsal-fin insertion, slightly in front of fin apex; free rear tip in front of lower caudal-fin origin by a distance about equal to its inner margin length; posterior margin slanting very slightly anterodorsally and then abruptly posterodorsally. Anal fin base expanded anteriorly as short preanal ridges, less than a quarter length of rest of base. Anal-fin base 0.81 (0.66–0.96) in anal–caudal space; height 1.47 (1.21–1.52) in base; inner margin 1.41 (1.21–1.52) in height, 2.08 (1.75–2.34) in base.

Caudal fin narrow-lobed and asymmetrical, with short

Table 2. Vertebral counts and ratios for the holotype (IPMB 38.14.02) and ranges for the 13 paratypes of *Glyphis fowlerae* sp. nov. Counts from the paralectotype of *G. gangeticus* and the holotype of G. siamensis are also provided.

	G. fowlerae sp. nov.			*G. gangeticus*	*G. siamensis*
				Paralec.	Holotype
	Holotype	Paratypes (n=12)		MNHN	NMW
		Min	Max	1141	61379
TL	577	487	778	556	630
Vertebrae:					
MP	65	60	67	50	66
DP	47	43	52	30	51
DC	91	82	96	89	92
PC	112	108	114	80	117
TC	203	196	209	169	209
%MP	32.0	30.0	33.2	29.6	31.6
%DP	23.2	21.8	26.0	17.8	24.4
%DC	44.8	41.8	45.9	52.7	44.0
%PC	55.2	54.1	58.2	47.3	56.0
DP/MP	0.72	0.66	0.87	0.60	0.77
DC/MP	1.40	1.28	1.48	1.78	1.39
A ratio	126.2	108.8	142.3	159.5	153.7
B ratio	71.2	48.8	72.5	100.0	74.6

terminal lobe and prominent, long, narrowly expanded, non-falcate ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave just anterior to subterminal notch, with prominent lateral undulations; preventral margin moderately convex, tip of ventral caudal-fin lobe bluntly pointed or narrowly rounded; lower postventral margin convex; upper postventral margin nearly straight except for convex section at subterminal notch; notch between postventral margins deep, forming about a 90–120° angle; subterminal notch a narrow, deep slot; subterminal margin slightly concave, terminal margin slightly concave where not damaged, lobe formed by these margins angular, tip of tail bluntly pointed or narrowly rounded and angular. Length of dorsal caudal margin 2.94 (2.77–3.08) in precaudal length, preventral caudal margin 2.35 (2.11–2.40) in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 3.35 (3.27–4.11) in dorsal caudal margin, subterminal margin length 1.32 (1.28–2.49) in terminal margin.

Vertebral counts listed in Table 2. Counts of total vertebral centra (TC) 203 (196–209 in 12 paratypes), precaudal centra (PC) 112 (108–114), monospondylous precaudal (MP) centra 65 (60–67), diplospondylous precaudal (DP) centra 47 (43–52), diplospondylous caudal (DC) centra 91 (82–96); MP centra 32.0 (30.0–33.2)%, DP centra 23.2 (21.8–26.0)%, and DC centra 44.8 (41.8–45.9)% of TC centra. Ratios of DP/MP centra 0.72 (0.66–0.87), DC/MP centra 1.40 (1.28–1.48), `A' ratio 126.2 (108.8–142.3), `B' ratio 71.2 (48.8–72.5). Transition between MP and DP centra about over pelvic-fin bases and just behind pelvic girdle. Last few MP centra before MP-DP transition not enlarged and not forming a 'stutter zone' of alternating long and short centra.

COLORATION.— When fresh and in preservative: Medium grey on dorsal surface of sides of head, trunk, and tail, shading to paler grey on the flanks, abruptly creamy white on lateral and ventral surfaces and lower base of caudal fin, eye pupil black. Demarcation of pale lower and dark upper surface (waterline) of head at level of nostrils and lower edge of eye, extending to about mid-height of gill openings; a more or less conspicuous narrow light ring around eyes; gill septa dark on their upper thirds but with their margins and lower surfaces whitish; flanks grey over pectoral-fin bases but shifting to whitish above pectoral-fin rear tips and over pelvic fins; a short, inconspicuous, and weakly defined light line extending from pelvic base onto mid-flank; precaudal tail grey above lateral line, much paler below it, bicolour extending onto caudal-fin base. Pectoral fins with a conspicuous rounded-angular dusky patch on dorsal surface of base, demarcated anteriorly at fin origin by abrupt white patch that extends to gills; dorsal pectoral fin web below and posterior to dark basal spot pale greyish, without light or dark markings; underside of pectoral whitish with pale dusky margin. Dorsal surfaces of pelvic fins with a dusky basal patch surrounded by

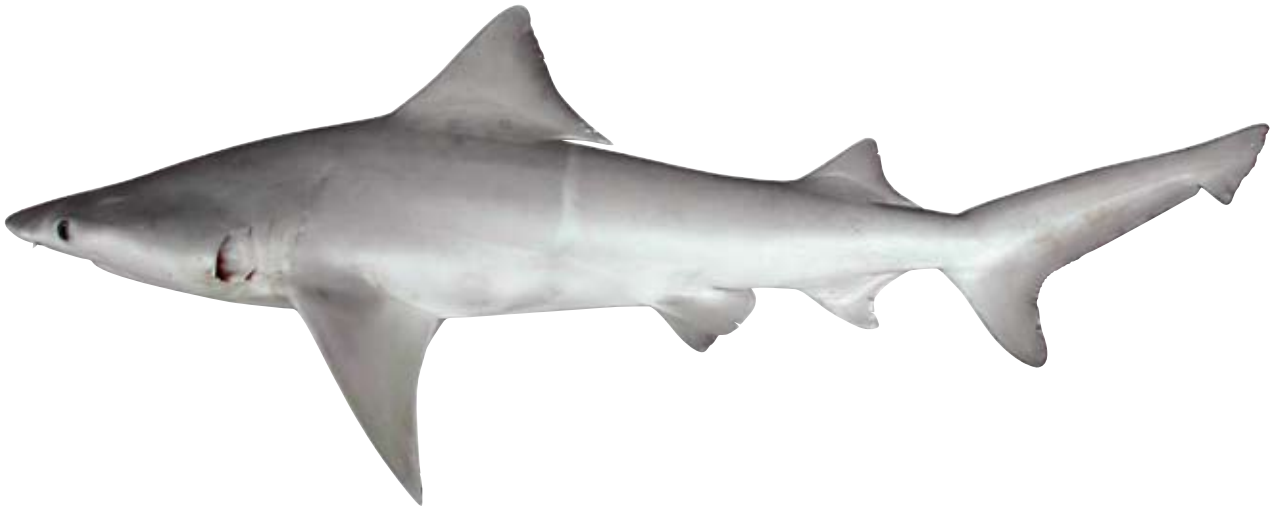

Figure 5. Lateral view of juvenile male *Glyphis* sp. (NSFEP BO471, 610 mm TL, fresh).

white, fin web whitish-grey, underside of fins and claspers white with light whitish grey web. First dorsal fin with a dusky grey base, conspicuous paler whitish-grey web with paler area on the free rear tip and a dusky margin; second dorsal fin with a similar highlighted fin web but with a broader dusky apex and posterior margin. Anal fin mostly whitish, sometimes with a dusky to blackish posterior web. Caudal fin medium grey with a white to pale greyish basal stripe that extends onto the hypaxial and epaxial fin web, preventral margin white, ventral lobe and postventral margin dusky to blackish, terminal lobe dusky or blackish, dorsal margin dusky.

BIOLOGY.— Essentially unknown; development presumably by placental viviparity as suggested by the newborn young and by reference to other, related carcharhinids, but adults of either sex including pregnant females were not available for examination.

SIZE.— Type specimens range in length from 487–778 mm TL, but these are all immature individuals and maximum total length of this species is probably between 2000 and 3000 mm, by comparison with species of *Carcharhinus*. Specimens ranging in size from 487–582 mm TL possessed open umbilical scars indicating they were only recently born; specimens between 600 and 632 mm TL possessed closed umbilical scars; two specimens of 667 and 778 mm TL had no umbilical scars. Thus, size at birth in this species is likely to be about 490–580 mm TL.

DISTRIBUTION AND HABITAT.— All but one of the specimens were collected in the vicinity of Kampung Abai (05°41′ N, 118°23′ E), on the Kinabatangan River in eastern Sabah; the other specimen, deposited at the NMW in Vienna has no specific locality data within Borneo. The Kinabatangan River at this locality has very low banks that slope gradually down to a flat and muddy bottom (Manjaji, 2002a). Although there is little information available on the hydrology of the area, the Lower Kinabatangan Segama Wetlands RAMSAR site (available at http://www.sabah.gov.my/sabc/downloads/RIS_LKSW_2008.pdf) provides the following hydrological characteristics for the streams of the Kulamba Wildlife Reserve where Kampung Abai is located: salinity 1.7–1.9, pH 6.4–7.5, temperature 25.5–29.9°C, conductivity 27.6–31.2 µS/cm, total suspended solids 126.8–214.5 mg/L, dissolved oxygen 4.6–5.9 mg/L. The most important features to take note of are the very low salinity (practically freshwater) and high suspended solids. Despite extensive sampling effort throughout Sabah, Sarawak and Kalimantan, this species has not been collected elsewhere.

ETYMOLOGY.— The epithet acknowledges the considerable efforts of Dr Sarah Fowler (Nature Bureau, UK) who has dedicated a lifetime of work towards the conservation of sharks, and who led the first major study on the elasmobranchs of Sabah in 1996 which culminated in the discovery of this species. Vernacular: Borneo River Shark

CONSERVATION.— Not evaluated by the IUCN *Red List of Threatened Species* but four other members of this genus are listed as either Critically Endangered or Endangered, and the issues facing those species are similar to those facing *G. fowlerae*, especially given its apparently very restricted range and human impacts on its habitat. The extent of logging and the increasing development of palm-oil plantations within the region also add to the threatening processes. Thus, *G. fowlerae* is likely to fall into one of the highly threatened categories and its conservation status urgently requires assessment.

DISCUSSION

Glyphis fowlerae is clearly separable from its congeners by a combination of morphology, meristics and coloration, and also on a molecular level (G. Naylor, unpubl. data). The key characters which distinguish species of *Glyphis* are comparative heights of the dorsal fins, vertebral counts and teeth morphology. *Glyphis gangeticus* has the greatest intraspecific difference in dorsal-fin heights (lowest second dorsal-fin height about 0.46 times first dorsal-fin height) compared to *G. fowlerae* (0.54–0.68) and *G. garricki* (0.58–0.66). In contrast, *G. glyphis* has a relatively taller second dorsal fin and as a result, the least difference in dorsal-fin heights of 0.67–0.84.

Glyphis fowlerae has a high number of vertebrae (total centra 196–209, monospondylous centra 60–67, n=13) compared to *G. garricki* (137–151 and 44–50, n=14) and *G. gangeticus* (169 and 50, n=1), but much less than *G. glyphis* (213–222 and 69–73, n=8). The counts for the single known specimen of *G. siamensis* (total centra 209, monospondylous centra 66) fall within the range of *G. fowlerae*, but they differ on a number of morphometric characters discussed later. *Glyphis fowlerae* has a higher tooth count (60–63, n=5) than *G. siamensis* (58, n=1), *G. glyphis* (53–58, n=4), but similar counts to *G. gangeticus* (62–71, n=3) and *G. garricki* (62–68, n=15).

Glyphis gangeticus was described by Müller & Henle in 1839 and in that description two syntypes were referred to: one dried specimen deposited in the Berlin Museum (ZMB 4474) and one in alcohol in the Paris Museum (MNHN 1141). Although their description is possibly based on both specimens, it is clear that the larger dried adult male specimen, ZMB 4474, was the one from which data was taken by Müller & Henle (1839), based on the larger size of this specimen (1850 vs. 556 mm TL). The illustration provided in the description is also clearly of an adult male also referable to the ZMB specimen. We designate the dried specimen (ZMB 4474) as the lectotype of *Glyphis gangeticus* and the smaller specimen in alcohol (MNHN 1141) as a paralectotype. Although it is often difficult to obtain accurate measurements from dried specimens, the few comparable measurements obtained from the original description were very similar to those recorded for the dried specimen despite a substantial increase in total length, probably due to overstretching of the skin (1700 mm TL fresh vs. 1850 mm TL dry).

Figure 6. Lateral view of head of juvenile male *Glyphis* sp. (NSFEP BO470, 658 mm TL, fresh).

In addition to the differences provided above, *G. fowlerae* further differs from *G. gangeticus* (based on both types) in having a longer snout (prenarial length 4.8–5.3 vs. 3.6–4.6% TL, preoral length 7.5–8.3 vs. 6.5–6.6% TL, preorbital length 8.3–10.5 vs. 7.0–7.7% TL), a shorter pelvic midpoint to second dorsal-fin origin measurement (5.5–7.7 vs. 9.4% TL), a slightly stockier head, body and tail (interorbital width 11.5–12.7 vs. 10.4–10.9% TL, head width 12.3–17.2 vs. 11.5% TL, trunk width 11–15.3 vs. 9.4% TL, caudal peduncle width 3.1–4.7 vs. 2.3% TL), shorter pectoral-fin posterior margin (12.8–15.0 vs. 17.2–18.4% TL), and a slightly shorter lower postventral caudal margin (4.4–5.5 vs. 5.9–6.2% TL). The specimens of *G. gangeticus* examined also have some of the lower teeth visible when the mouth is closed, whereas in the new species, the lower teeth are all concealed by the lips when the mouth is closed.

Glyphis fowlerae can be distinguished from *G. glyphis* from northern Australia in having a longer snout (prenarial length 4.8–5.3 vs. 3.3–4.7% TL, preorbital length 8.3–10.5 vs. 6.3–7.5% TL) and nostrils further apart (internarial width 7.0–7.7 vs. 5.2–6.6% TL). It can also be distinguished from *G. garricki* from northern Australia in having a slightly shorter and lower caudal-fin lobe (preventral caudal margin 10.8–12.3 vs. 12.7–13.9% TL, lower postventral margin 4.4–5.5 vs. 5.7–7.9% TL), a slightly shorter caudal terminal lobe (terminal lobe length 5.2–6.5 vs. 6.7–7.4% TL), first dorsal fin slightly closer to pectoral insertions (DPI length 4.0–5.9 vs. 6.1–7.0% TL), a taller caudal peduncle (caudal peduncle height 4.2–5.7 vs. 3.6–4.0% TL), a smaller pectoral fin (anterior margin 16.7–20.0 vs. 19.6–22.4% TL, posterior margin 12.8–15.0 vs. 15.6–19.6% TL), and a lower pelvic fin (pelvic-fin height 4.6–6.3 vs. 6.9–8.1% TL).

Comparison of the new species with *G. siamensis* is restricted to the unique holotype. *Glyphis fowlerae* differs from this specimen in having a longer snout (prenarial length 4.8–5.3 vs. 3.8% TL, preorbital length 8.3–10.5 vs. 7.8% TL), wider nostrils (nostril width 1.9–2.3 vs. 1.4% TL), taller pelvic fins (pelvic-fin length 8.8–10.3 vs. 7.0% TL), and a longer second dorsal-fin base (7.4–9.3 vs. 6.7% TL).

Two specimens of *Glyphis* collected from Mukah in

Figure 7. Lateral view of adult male lectotype of *Glyphis gangeticus* (ZMB 4474, 1850 mm TL, dried).

Sarawak during recent National Science Foundation (NSF)-funded surveys are clearly distinguishable from *G. fowlerae*, based on several morphometric characters, and they also exhibit substantial DNA sequence divergence in the mitochondrial marker NADH2 (G. Naylor, pers. comm., Florida State University). This species has since been temporarily identified as *Glyphis* sp. (Compagno *et al*., 2008). Unfortunately, on a recent trip to Kuching (Nov. 2009) to examine these specimens, they could not be located and we consider both specimens missing, possibly lost. Based on an image of a fresh specimen of *G*. sp. (Fig. 5), it differs from *G. fowlerae* in having larger eyes, a much taller first dorsal fin, a greater first dorsal-fin height vs. second dorsal-fin height ratio, a more concave second dorsal-fin posterior margin, the waterline extending through mid-level of eye (vs. below eye), possibly larger pectoral fins, and appears to be less stocky. The large (1660 mm TL) adult male *Glyphis* recorded from Sampit Bay (Central Kalimantan) by Fahmi & Adrim (2009) has a much taller first dorsal fin and a relatively low (compared to congeners) second dorsal fin. This species appears to be much closer to, and possibly an adult of, *G*. sp. recorded from Mukah, rather than being conspecific with *G. fowlerae*. Although the first dorsal fin is relatively taller than in the juvenile specimen of *G*. sp., this difference is probably due to ontogenetic change similar to that observed in *G. garricki* and *G. glyphis* from northern Australia where large specimens have much larger first dorsal and pectoral fins than juveniles. Based on relative dorsal-fin heights, *Glyphis* sp. is clearly distinct from *G. garricki*, *G. glyphis* and *G. fowlerae*, and is closer to *G. gangeticus* and *G. siamensis* from the northern Indian Ocean. Specimens of this species need to be accessed to determine whether it is conspecific with *G. gangeticus* or *G. siamensis*, or whether it is undescribed.

A publication by Roberts (2006b) suggested that the type locality of *G. gangeticus* is likely to be from 'the lower Sundarbans south of Kulna, and relatively near to the sea, in what is now Bangladesh'; thus from brackish rather than freshwater as originally suggested. Roberts (2006b) also suggested that *G. siamensis* is a junior synonym of *G. gangeticus*, but vertebral counts and tooth counts collected by the senior author do not support this argument and *G. siamensis* should provisionally be considered as a valid nominal species. Roberts (2006b) reported on numerous specimens of *G. gangeticus* collected (by the author) from marine habitats in the Bay of Bengal, off Bangladesh and Myanmar, suggesting a preference for marine rather than riverine habitats as previously thought. However, the validity of these findings must be brought into question based on the following error in this manuscript. Roberts (2006b, Figure 7) provided images of 3 fresh juvenile specimens of *G. gangeticus* (one deposited at MNHN in Paris and one at the AMS in Sydney, AMS I 43504–001), but they are clearly misidentifications of the Bull Shark, *Carcharhinus leucas* (Müller & Henle, 1839). This was confirmed by examination by one of us (WW) of images of the AMS specimen which are clearly *C. leucas*. Although some other images provided in Roberts (2006b) are of *Glyphis gangeticus*, these misidentifications of juvenile sharks raises concern over the validity of identifications by this author of a large collection of jaws as *G. gangeticus*. Thus, the findings of his paper need to be treated somewhat cautiously which is unfortunate, given the general lack of knowledge on this group of sharks.

Roberts (2006a) provided a note on a set of *Glyphis* jaws from Pulo Condor off the Vietnam coast (ZMB 14850) that he considered to be from *G. glyphis*, which would be a large range extension from the known range of northern Australia and Papua New Guinea. He also suggested that the dried holotype was probably collected from either the Ganges delta or off the Sundarbans (Bangladesh). Further investigation of *G. glyphis* is required to determine the extent of its range and to determine whether it may also occur in waters between these known localities, e.g. off Borneo or Indonesia.

Comparative material.

Carcharhinus leucas: AMS I 43504–001, female 863 mm TL, Sittway market, Rakhine district, Bay of Bengal, Myanmar, May 2004 (identified as

G. gangeticus in Roberts (2006b).
Glyphis gangeticus: ZMB 4474 (lectotype), adult male 1850 mm TL, according to Müller & Henle (1839) "Im Ganges, 60 Stunden oberhalb des Meers bei Hougly gefangen." (In the Ganges, captured in the Hooghly River 60 leagues above the sea, if correct possibly near the city of Navadwip at ca. 23º24′ N, 88º22′ E) photos and measurements contributed by Dr. H. Paepke of the Humboldt Museum, Berlin; MNHN 1141 (paralectotype), juvenile male 556 mm TL, "Bengal"; ZSI 8067, newborn female 610 mm TL, Hooghly River, West Bengal, India. ZMB 4474 was considered as lost (Garrick, 1982, 1985, Compagno, 1984, 1988) but was later rediscovered (Paepke & Schmidt, 1988).
Glyphis garricki: CSIRO H 5262–01 (holotype), female 670 mm TL, East Alligator River, Kakadu National Park, Northern Territory, 12°07′ S, 132°38′ E, 09 Jun. 1999; CSIRO H 6173–01 (jaws), female 1770 mm TL, northeast of entrance to Cambridge Gulf, Western Australia, 14°42′ S, 128°34′ E, 22 Oct. 2003; CSIRO H 6635–01 (jaws), adult male ca. 1450 mm TL, South Alligator River, 3 km downstream from 12º39′ S, 132º29′ E, 11 m depth, 10 May 1996; LWF–E227, juvenile male 720 mm TL, LWF–E294, juvenile male 720 mm TL, New Guinea (specimens lost but radiographs, drawings and photos provided by Prof. J.A.F. Garrick); LWF–E217 (jaws, supplied by P. Kailola), adult male ca. 1500–1700 mm TL, LWF–E219 (jaws, supplied by J.A.F. Garrick), Port Romilly, New Guinea, 07°40′ S, 144°50′ E, 12 Mar. 1966; LWF–E473 (jaws, supplied by P. Kailola), 1020 mm TL, Baimuru, New Guinea, 07°33′ S, 144°51′ E, 28 Mar. 1974; SAM uncatalogued (previously WAM P 32600–001) (chondrocranium, jaws, pelvic fin skeleton, pectoral girdle), juvenile female 1350 mm TL, King Sound, Western Australia, ca. 17°13′ S, 123°40′ E, 09 Jun. 2003; WAM P 32598–001, juvenile male 906 mm TL, Doctors Creek, Derby, Western Australia, 17°13′ S, 123°40′ E, 07 Jun. 2003; WAM P 32599–001, female 957 mm TL, Doctors Creek, Derby, Western Australia, 17°13′ S, 123°40′ E, 06 Jun. 2003; WAM P 32600–001 (3 specimens), adult male 1418 mm TL, juvenile male 1191 mm TL, juvenile male 1022 mm TL, King Sound, Western Australia, ca. 17°13′ S, 123°40′ E, 09 Jun. 2003; WAM P 32597–001, (deformed) adolescent male 994 mm TL, Doctors Creek, Derby, Western Australia, 17°13′ S, 123°40′ E, 2002. Also, data on specimen not seen but reported by Taniuchi et al. (1991), juvenile female 1314 mm TL, 100 km up from the mouth of the Adelaide River, Northern Territory, Australia, 13°00′ S, 131°15′ E, 26 May 1989.
Glyphis glyphis: CSIRO H 5261–01, juvenile male 770 mm TL, East Alligator River, Kakadu National Park, Northern Territory, 12°12′ S, 132°47′ E, 1–3.5 m, 10 Jun. 1999; CSIRO H 5756–01, juvenile male 631 mm TL, Marrakai Creek, Adelaide River, Northern Territory, 12°41′ S, 131°20′ E, 28 Nov. 2001; NTM S 15097–001, juvenile male 792 mm TL, Brooks Creek, South Alligator River, Kakadu National Park, Northern Territory, 12°12′ S, 132°24′ E, 04 Jun. 1999; NTM S 15351–001, female 678 mm TL, Marrakai Creek, Adelaide River system, Northern Territory, 12°41′ S, 131°20′ E, 11 Sep 2001; NTM S 15508–001, female 595 mm TL, NTM S 15508–002, juvenile male 590 mm TL, Adelaide River system, Northern Territory, 12°37′ S, 132°47′ E, 16 Nov. 2002; NTM S 16217–001, adolescent male 1447 mm TL, Wenlock River, Cape York Peninsula, Queensland, 12°03′ S, 141°55′ E, 01 Feb. 2006; QM I 19719, juvenile male 745 mm TL, 17 km upstream from Bizant River mouth, Princess Charlotte Bay, Queensland, 14°33′ S, 144°05′ E, 23 Mar. 1982; QM I 36881, female 1095 mm TL, QM I 36882, juvenile male 705 mm TL, QM I 36883, juvenile male 867 mm TL, QM I 36884, juvenile male 723 mm TL, QM I 36885, 770 mm TL, Gloughs Landing, Wenlock River, Queensland, 12°45′ S, 142°59′ E, 28 Apr. 2005; LWF–E218 (jaws), juvenile female ca. 1600–1800 mm, Port Romilly, New Guinea, 07°40′ S, 144°50′ E, 12 Mar. 1966; LWF–E405B (jaws, supplied by P. Kailola), ca. 1700–1800 mm, Alligator Island, Fly River, New Guinea, 07°19′ S, 141°11′ E; ZMB 5265 (holotype), stuffed specimen, juvenile female 1023 mm TL, locality unknown but probably Indian Ocean (photos, morphometrics and radiographs of tail from Dr. H. Paepke).
Glyphis siamensis: NMW 61379 (holotype), juvenile male 630 mm TL, Irrawaddy River mouth, Rangoon, Myanmar, photos, radiographs and measurements contributed by Dr. Ernst Mikschi, Vienna Museum.
Glyphis sp.: NSFEP BO470, juvenile male 658 mm TL, NSFEP BO471, juvenile male 610 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 29 Apr. 2004, specimens were not found during a trip to the IPPS location by one of the authors (WW) in November 2009.

Key to the nominal species of *Glyphis*

1 Second dorsal fin relatively low, about half height of first dorsal fin 2
Second dorsal fin relatively large, more than half height of first dorsal fin 3

2 Total vertebral count 209; tooth row count 58 (from only known specimen)..... .....*G. siamensis* (Myanmar)
Total vertebral count 169 (from one specimen); tooth row count 62–71 ..... *G. gangeticus* (India, Pakistan)

3 Total vertebral count more than 210, monospondylous count more than 68; total tooth row count less than 59; black blotch at ventral tip of pectoral fins .... *G. glyphis* (northern Australia, New Guinea)
Total vertebral count less than 210, monospondylous count less than 67; total tooth row count more than 60; no black blotch at ventral tip of pectoral fins 4

4 Total vertebral count 196–209, monospondylous count 60–67; waterline (demarcation of dark upper and pale lower surfaces) at level of lower eye on head ..... *G. fowlerae* (Sabah, Borneo)

Total vertebral count 137–151, monospondylous count 44–50; waterline (demarcation of dark upper and pale lower surfaces) at a level greater than an eye diameter below lower level of eye ..... *G. garricki* (northern Australia, New Guinea)

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Resurrection and redescription of the Borneo Broadfin Shark *Lamiopsis tephrodes* (Fowler, 1905) (Carcharhiniformes: Carcharhinidae)

William T. White[1], Peter R. Last[1], Gavin J.P. Naylor[2] & Mark Harris[3]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Florida State University, School of Computational Science/Department of Biological Science, Tallahassee, FL 32304, USA
[3] F.F.C., New Port Richey, Florida, USA

ABSTRACT.— The genus *Lamiopsis* was previously considered to be monotypic, represented by a single species *L. temminckii*. Recent molecular analyses from across the range of this genus has shown that two species should be recognised, one in the Indian Ocean centred around India and another in the Western Central Pacific centred around Borneo. *Lamiopsis tephrodes* (Fowler, 1905) was described from Borneo and is resurrected from being a junior synonym of *L. temminckii* to a valid species. A redescription of *L. tephrodes*, based largely on recently collected material is provided. This species differs from *L. temminckii* in dentition, some morphological characters and possibly size. It also exhibits substantial DNA sequence divergence in the mitochondrial marker ND2. A lectotype is also herein designated for *L. temminckii*. The conservation of these species needs to be reassessed, with both species likely to fall in one of the highly threatened IUCN Red List categories.

Key words: *Lamiopsis temminckii* – *Lamiopsis tephrodes* – Borneo – resurrection – redescription – threatened

PDF contact: william.white@csiro.au

INTRODUCTION

The genus *Lamiopsis* was proposed by Gill (1862) for *Carcharias (Prionodon) temminckii* Müller & Henle, 1839 which was described from several specimens from Pondicherry in India. Prior to the 1970s, this genus was often synonomised with *Carcharhinus*, but was considered valid by Compagno (1970, 1979, 1984, 1988) and Garrick (1982). The genus *Lamiopsis* shares many of the key characteristics with the genus *Glyphis* Agassiz, 1843 which, in combination, distinguishes them from other carcharhinid genera, e.g. dentition, large second dorsal and pectoral fins, and longitudinal (rather than crescentic) precaudal pits. *Lamiopsis* differs from *Glyphis* in having a nearly straight anal-fin posterior margin, larger and more ventrolaterally situated eyes, longer snout and more posterior first dorsal fin (Compagno, 1988).

Lamiopsis tephrodes was described by Fowler (1905) as *Carcharhinus tephrodes* based on two specimens collected from off Baram in Sarawak (Borneo), a ~637 mm holotype and a ~372 mm paratype. Fowler (1905) did not define the characteristics that distinguish *L. tephrodes* from *L. temminckii*. Garrick & Schultz (1963) synonomised *L. tephrodes* with *L. temminckii*, and although Fowler (1930, 1941, 1968) retained *L. tephrodes*, examination of the types by Compagno (1979, 1988) revealed nothing to separate the species. Fowler (1941, 1968) synonomised *Carcharias sealei* Pietschmann, 1913 with *L. tephrodes*, and listed *C. borneensis* (Bleeker, 1858) as a doubtful synonym. However, *C. sealei* and *C. borneensis* are both considered valid *Carcharhinus* species and are not congeneric or conspecific with *L. tephrodes* (Compagno, 1979). Fowler's misidentification is possibly due to the paratype of *L. tephrodes* not being a *Lamiopsis* species, and hence not congeneric or conspecific with the holotype. Instead, the paratype of *L. tephrodes* represents an undescribed *Carcharhinus* species of the '*C. porosus*' group (Compagno, 1979, 1988), i.e. *Carcharhinus* sp. A [*sensu* Compagno *et al*., 2005].

The collection of fresh specimens of *Lamiopsis* during recent surveys throughout South-east Asia has allowed for more detailed taxonomic and molecular comparisons of this genus throughout its range. The present account reviews the nominal species of *Lamiopsis*, resurrects *L. tephrodes* as a valid taxon and provides a detailed redescription of this species. One of the syntypes of *L. temminckii* is also designated as a lectotype.

METHODS

Measurement terminology follows Compagno (1984, 1988, 2001) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Dentitional terms generally follow Compagno (1979, 1988, 2001). Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1979, 1988, 2001).

A total of 11 *Lamiopsis tephrodes* were measured in full (Table 1). A subsample of measurements from the dried lectotype of *Lamiopsis temminckii* (BMNH 1851.8.16.11) was also taken. Morphometric ranges of the 11 measured specimens of *L. tephrodes* are provided in the descriptive section. Meristics were taken from radiographs of 4 specimens of *L. tephrodes* (CSIRO H 6662–01, CSIRO H 6137–07, CSIRO H 7083–01 and CSIRO H 7084–01). Counts were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of upper lobe of caudal fin) and caudal (centra of the caudal fin) vertebrae. Tooth row counts were taken in situ or from excised jaws of 8 specimens of *L. tephrodes* and 7 specimens of *L. temminckii*.

Muscle tissue samples were taken from specimens collected in the field and stored in either 95% ethanol or DMSO until processed in the laboratory. Total DNA was extracted from the tissue samples using High Pure PCR Template Preparation Kit (Roche Diagnostics). Extracted total DNA was stored at -20° C. Sub-sets of the extracted template were diluted to 1/10 of original strength and stored for subsequent use in PCR reactions. Samples were PCR amplified using Hot Start Taq (Promega) using primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (Naylor *et al*., 2005). These primers are designed to bind to the ASN and ILE tRNA regions flanking the NADH2 gene in the mitochondrial genome of elasmobranchs. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of Taq, PCR buffer, 2.5 mM of $MgCl^2$, 1.0 mM of DNTPs, and 1.0 mM of each primer. The reaction cocktail was denaturised at 94°C for 3 minutes, after which it was subjected to 35 cycles of 94°C /30s, 48°C /30s and 72°C /90s followed by an indefinite hold in the thermal cycler at 4°C.

A sample of the completed PCR reaction was run on 1% agarose gels, stained, visualised and photographed under UV light to assess the success of PCR amplification. Samples with successful amplification products were purified using purification plates (Millipore, MA) attached to a vacuum manifold. The purified PCR products were quantified and diluted to between 30–100 ng/µl and subsequently sent to SeqWright (Houston, TX) for sequencing. The software packages Phred and Phrap were used to read sequence traces, assign quality values, make base calls and produce output files for subsequent alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment.

The aligned nucleotide sequences were subjected to Phylogenetic analysis using PAUP* (v4.0b106). The data were subjected to Neighbour joining based on K2P Distance, Parsimony and Maximum Likelihood analysis using parameter optimised models that best fit the data. The topologies across all methods were consistent with each other.

Specimens are referred to by the following prefixes for their registration numbers: BMNH, British Museum of Natural History, London; CSIRO, Australian National Fish Collection, Hobart; IPPS, Institut Penyelidikan Perikanan Sarawak, Kuching, Malaysia; RMNH, Rikjsmuseum van Natuurlkjke Histoire, Leiden; PMH, Mark Harris personal collection. In the molecular trees, field codes (prefixed by BO, DF or KA) are provided for samples collected by Drs J. Caira and K. Jensen, and data and images for these specimens are available at http://tapeworms.uconn.edu.

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus *Lamiopsis* Gill, 1862

Type species. *Carcharias (Prionodon) temminckii* Müller & Henle, 1839

SPECIES.— *Lamiopsis* includes two nominal species: *L. temminckii* (Müller & Henle, 1839); *L. tephrodes* (Fowler, 1905). *Carcharhinus microphthalmus*, described by Chu (1960), is likely to be a synonym of *L. tephrodes*.

Lamiopsis tephrodes (Fowler, 1905)

Figs 1–6, Table 1

Carcharhias (Prionodon) temminckii (non Müller & Henle): Martens, 1876: 409 (Makassar Strait).
Carcharhinus tephrodes Fowler, 1905: 455–458, fig. 1 (Type locality: Baram, Borneo).
Eulamia tephrodes: Fowler, 1930: 493 (Java).
Eulamia temminckii: Fowler, 1930: 493 (Java).
Carcharhinus microphthalmus Chu (Zhu), 1960: 84, figs 78, 79 (Type locality: Jia-bo, China).
Lamiopsis temmincki (in part, non Müller & Henle): Compagno, 1979: 542, 543 (Makassar Straits and Borneo).

Material examined. 17 specimens: CSIRO H 6137–07, juvenile male 600 mm TL (dorsal, pectoral and lower

caudal fins missing), Muara Baru fish landing site, Jakarta, Indonesia (caught from southern Kalimantan according to fisheries information), 31 Jan. 2003; CSIRO H 6662–02, juvenile male 408 mm TL, Muara Baru fish landing site, Jakarta, Indonesia (caught from southern Kalimantan according to fisheries information), 19 Apr. 2004; CSIRO H 7083–01, female 542 mm TL, Kota Baru, South Kalimantan, Indonesia, 03°14.45′ S, 116°13.24′ E, 28 Nov. 2006; CSIRO H 7084–01, female 570 mm TL (finless and cut along dorsal midline), Desa Bunyu, Pulau Bunyu, East Kalimantan, Indonesia, 03°27.31′ S, 117°50.34′ E, 22 Jul. 2008; IPPS 28404–11, female 706 mm TL, IPPS WWPLAL#7, juvenile male 789 mm TL, IPPS WWPLAL#8, female 806 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 28 Apr. 2004; IPPS 08–18, adult male 1282 mm TL, IPPS 08–19, subadult male 1080 mm TL, Batang Lupar, Sarawak, Malaysia, 01°25′ N, 111°06′ E; 26 May 2008; IPPS BO259, juvenile male 710 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 20 May 2003; IPPS HBO1, juvenile male 765 mm TL, Sarawak, Malaysia, 2002; RMNH 4292, female 493 mm TL, Borneo; RMNH 4293, juvenile female 450 mm TL, Borneo; PMH 293–1 (jaw only), female 1235 mm TL, PMH 293–2 (jaw only), female 1250 mm TL, PMH 293–3 (jaw only), male 1280 mm TL, Penang, Malaysia; PMH 293–4 (jaw only), unsexed ~1250–1300 mm TL, Phuket, Thailand.

DIAGNOSIS.— A species of *Lamiopsis* with the following combination of characters: a moderately long snout; similarly-sized dorsal fins; lips mostly concealing teeth when mouth is closed, except near symphysis; upper anterior teeth broadly triangular, serrated; lower anterior teeth long, narrow, erect, with non-hastate cusps which are either smooth or finely serrated; tooth row counts 33–40/34–40; interdorsal space 16.2–20.4% TL; pectoral-fin anterior margins weakly convex, its length 12.4–14.4% TL; pelvic fin anterior margins 7.4–9.3% TL and 48–53% of pectoral anterior margin; first dorsal fin relatively small, raked, subtriangular, with nearly straight to shallowly concave posterior margin its free rear tip just anterior to pelvic-fin origins, length 14.9–17.1% TL, height 5.6–8.1% TL; second dorsal fin large, subtriangular, almost as high as first dorsal fin, length 11.8–14.3% TL, height 4.8–7.3% TL and 83–93% of first dorsal-fin height; anal fin height 3.8–5.6% TL and 70–85% of second dorsal-fin height, base 78–98% of second dorsal-fin base; total vertebral centra 174–181, precaudal counts 98–100, monospondylous precaudal centra 50–51 and 28–29% of total centra, diplospondylous precaudal centra 48–49 and 27–28% of total centra, diplospondylous caudal counts 75–81 and 43–45% of total counts; demarcation of light and dark colour surfaces (waterline) on head strong, extending from lateral angle of snout to upper margin of eye, dark surface not visible in ventral view of head; fins lacking distinct black or white tips or markings.

DESCRIPTION.— Body stout, trunk subcircular and almost pear-shaped in section at first dorsal-fin base, length of trunk from fifth gill slits to vent 1.06–1.35 times head length. Predorsal, interdorsal and postdorsal ridges absent from midline of back, lateral ridges absent from body. Caudal peduncle stout, rounded-hexagonal in section at second dorsal-fin insertion, postdorsal and postventral spaces flattened and often with a shallow median groove anteriorly, lateral surfaces subangular and with a broad, low, inconspicuous lateral ridge on each side at middle of the peduncle that extends anteriorly to anal-fin origin and posteriorly onto the caudal-fin base; height of caudal peduncle at second dorsal-fin insertion 1.10–1.61 times its width, 1.29–1.64 times in dorsal–caudal space. Precaudal pits present; upper pit a shallow, subtriangular depression, not arcuate and crescentic; lower pit rudimentary or absent, essentially a dimple at the lower caudal-fin origin.

Head length to fifth gill opening 0.73–0.85 times in pectoral–pelvic space. Head broad, moderately long, flattened anteriorly, ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, nearly straight on snout, weakly convex above eye, moderately concave at nape and convex above gills, convex ventrally along lower jaws and beneath gills. In dorsoventral view, head narrowly parabolic, with gill septa expanded outwards. Snout moderately long, preoral snout length 0.73–0.89 times mouth width; tip moderately rounded in dorsoventral view and with a weak angle at nostrils but not noticeably indented anterior to nostrils; snout bluntly pointed in lateral view, weakly convex above and below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, with height 0.97–1.18 in eye length. Eyes very small, length 12.2–23.2 in head length; situated mostly laterally and at about level of head rim; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches and secondary lower eyelids fused to upper eyelids.

Spiracles absent. First three gill openings subequal in height, fourth and fifth increasingly smaller, fifth about 0.72–0.99 of height of third; height of third about 6.01–8.74 in head length and 1.39–3.58 times eye length. Margins of gill openings nearly straight, posterior margins irregular; first three openings upright, fourth and fifth sloping slightly posterodorsally from lower edges. Gill filaments not visible from outside. Upper end of highest gill opening just above level of upper edge of eye. Gill-raker papillae absent from gill arches.

Nostrils with very large oval incurrent apertures; prominent triangular anterior nasal flaps with narrowly pointed tips, mesonarial flaps absent, small suboval excurrent apertures, posterior nasal flaps absent; well in front of mouth; width 1.98–2.36 in internarial width, 0.55–0.93 in eye length, 1.33–1.91 in longest gill-opening.

Mouth broadly arched and large; margin of lower jaw

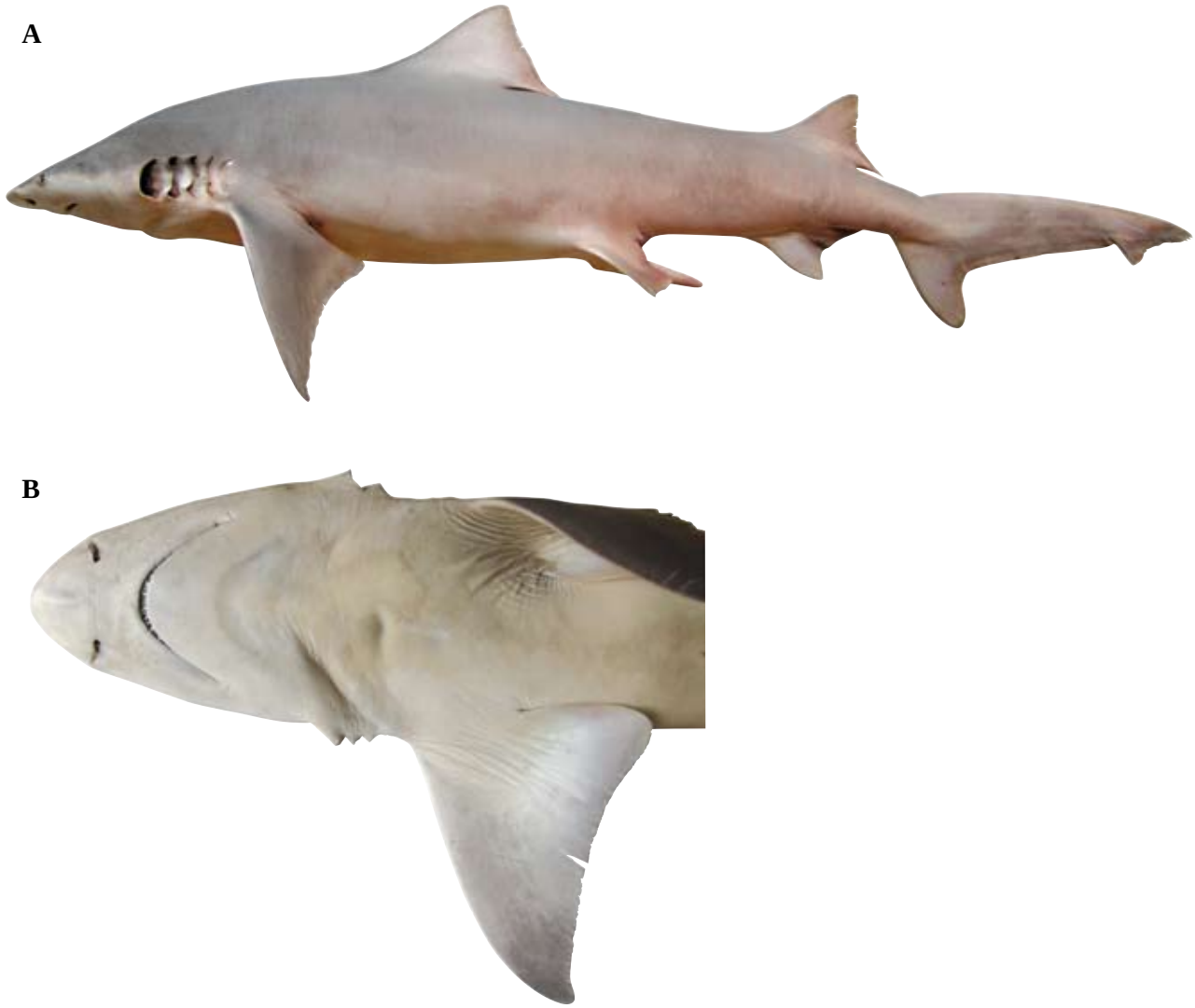

Figure 1. Adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL): A. lateral view (fresh); B. anterior ventral view (left pectoral not in view, preserved).

slightly less convex near symphysis; width 2.53–2.82 in head length; mouth length 1.67–1.91 in mouth width. Lips mostly concealing teeth when mouth is closed. Tongue large, flat and broadly rounded, filling floor of mouth. Maxillary valve narrow, width slightly less than eye diameter, strongly papillose. No large buccal papillae on floor or roof of mouth behind maxillary valve. Palate, floor of mouth and gill arches covered with buccopharyngeal denticles. Labial furrows short, uppers 0.69–1.15 times as long as lowers, lowers only barely concealed by overlapping upper lip; anterior ends of uppers far behind eyes by distance about 40% of mouth width.

Odontological meristics: 33–40/34–40 (n=8) with functional tooth series averaging 1–4/2–5, increasing in lower posteriors. Sexual dimorphism in dental morphology not evident; dignathic heterodonty strongly evident.

Monognathic heterodonty graduated but evident in upper jaw. Presence of 1–5 distinct, well developed medial teeth arranged asymmetrically and approximately one quarter height of medials in lower jaw. Upper teeth compressed, broadly triangular and not distinctly cordiform in shape; gradient serrations present, ascending from very fine at the apex of cusps to moderately coarse basally; distal and mesial shoulders somewhat pronounced on anterior teeth but less so in laterals, becoming more symmetrical with crown foot on mesial surface of posteriors and only slightly pronounced on distal surface; mesial root lobe noticeably shorter than distal root lobe in first two to three rows of anterior teeth, becoming more symmetrical laterally and subsequently reversing with posteriors having shorter distal lobes; contour of basal root edge on anterior teeth somewhat concave, becoming nearly straight-edged in laterally positioned teeth; cusps of first three to four rows of anterior teeth symmetrical with straight mesial and distal edges but mesial edges become more convex with lateral rows in series; distal

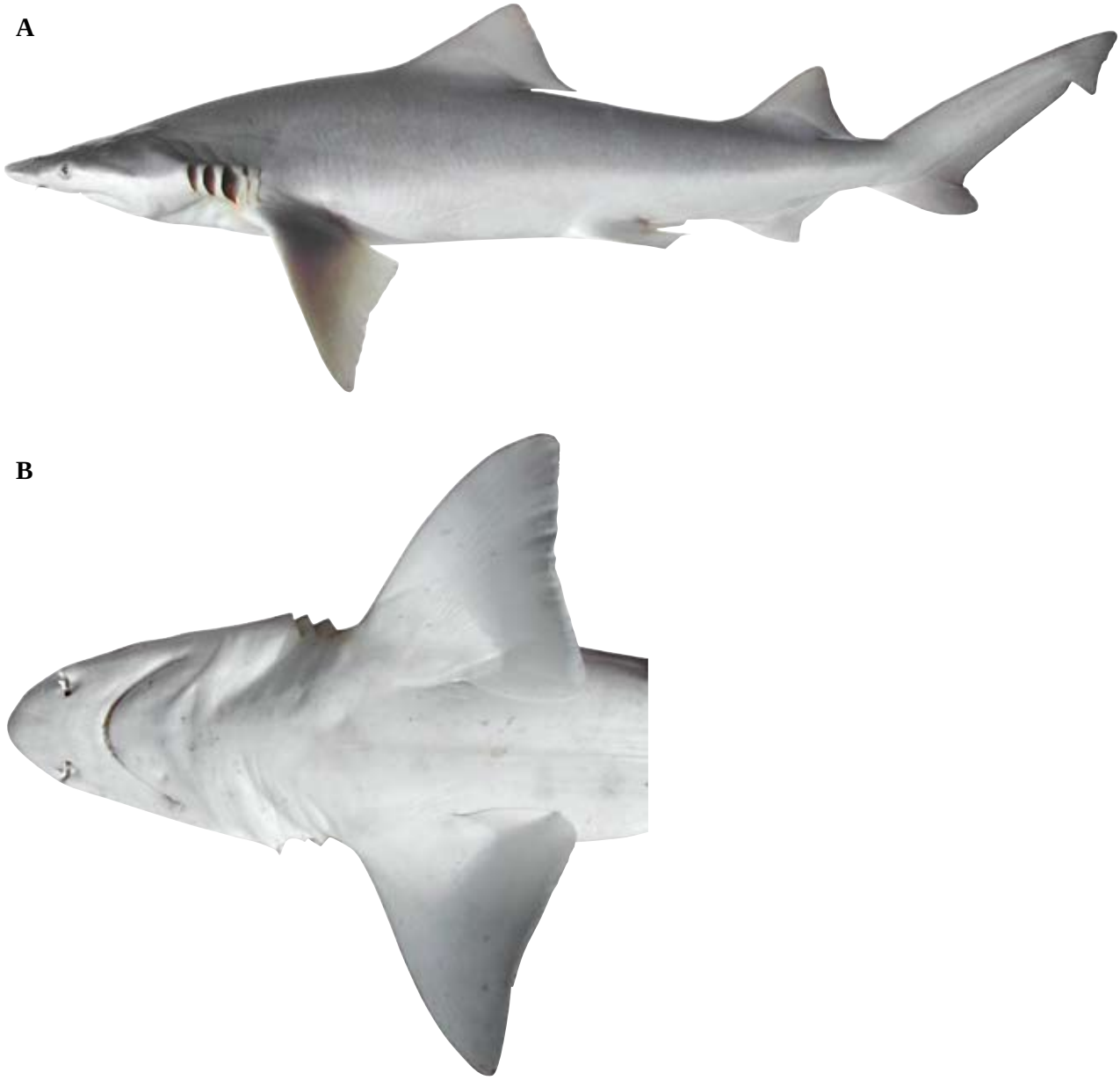

Figure 2. Female *Lamiopsis tephrodes* (not retained, 750 mm TL, Mukah, Sarawak, fresh): A. lateral view; B. anterior ventral view.

edges remain virtually straight except for posteriors; heterodonty more pronounced from lateral to posterior tooth positions; crown height and overall tooth size decrease abruptly in posteriors with the presence of approximately 3–5 rows of carinate molariforms; cusp retention at this level either weak or nonexistent.

Monognathic heterodonty graduated but evident in lower jaw. Presence of a single row of large, well developed, conical medial teeth not asymmetrically positioned; cusps of lower anteriors non-hastate with either smooth or extremely finely serrated cutting edge spanning entire length of cusp and reaching crown foot; cusps somewhat long and recurving lingually with apex slightly reflexed labially; basal ledges strongly pronounced on anterior teeth, becoming less protrusive laterally; roots of anterior teeth strongly arched, lobate and deeply concave with distal and mesial root lobes symmetrical and equal in size; cusps on lateral rows significantly shorter than anteriors, only slightly recurving lingually and with little or no reflexing of apex labially; cutting edges descend onto crown foot and distal shoulder; root lobes well developed and expanded laterally and are only weakly concave; heterodonty more pronounced from laterals to posteriors; crown height and overall tooth size decrease abruptly with the presence of 3 or more rows of semi-molariform teeth with blunt but variably developed cusps.

Lateral trunk denticles of adult male (IPPS 08–18) small, imbricate, transversely oval, with 5 short, stout cusps; crowns about 1.5 times wider than long, with 5

Table 1. Proportional dimensions as percentages of total length and ranges for 11 specimens of *Lamiopsis tephrodes*. The specimens are arranged in order of increasing size from left to right.

	CSIRO H 6662–02	RMNH 4293	RMNH 4292	CSIRO H 7083–01	CSIRO H 6137–07	IPPS 28404–11	IPPS HBO1	IPPS WWPLAL#7	IPPS WWPLAL#8	IPPS 08–19	IPPS 08–18	Min.	Max.
TOT	408	450	493	542	600	706	765	789	806	1080	1282	408	1282
PRC	75.7	76.4	75.9	75.5	74.5	75.4	75.2	74.8	74.3	75.2	75.5	74.3	76.4
PD2	61.0	61.8	60.3	61.1	59.8	59.9	60.7	59.6	60.5	59.5	61.1	59.5	61.8
PD1	32.3	33.1	33.3	33.1	32.0	32.0	31.9	33.2	32.6	31.9	31.4	31.4	33.3
HDL	24.4	24.9	25.4	24.2	23.9	24.0	23.0	23.2	23.9	22.9	21.9	21.9	25.4
PG1	20.5	20.4	20.8	20.2	19.1	20.0	19.0	19.3	19.7	18.6	18.0	18.0	20.8
POB	9.0	9.2	9.4	8.8	8.6	8.8	8.2	8.1	8.5	8.2	7.8	7.8	9.4
POB(horiz.)	7.1	7.5	7.9	6.8	7.2	7.0	7.0	7.0	7.3	6.3	6.6	6.3	7.9
POR	7.8	6.9	7.1	7.4	7.3	7.6	6.8	6.8	7.5	6.7	6.5	6.5	7.8
PRN	5.4	5.1	5.3	5.3	5.1	5.5	4.7	5.0	5.3	4.8	4.5	4.5	5.5
PRN(horiz.)	4.9	4.6	4.5	4.7	4.8	5.0	4.3	4.6	4.8	4.2	3.9	3.9	5.0
PP1	23.3	23.8	25.4	23.7	23.1	22.5	22.2	21.6	23.2	21.9	21.6	21.6	25.4
PP2	47.3	48.2	48.9	47.4	47.0	47.7	45.9	46.4	47.5	46.4	46.0	45.9	48.9
SVL	50.4	51.8	51.1	50.9	49.8	50.7	48.9	49.4	50.0	49.2	49.1	48.9	51.8
PAL	61.0	60.7	59.8	59.0	60.3	58.8	59.0	58.7	58.4	59.5	59.8	58.4	61.0
IDS	17.6	17.6	16.2	18.6	18.1	17.7	18.4	17.6	17.5	18.8	20.4	16.2	20.4
DCS	5.9	5.8	5.7	6.1	6.0	6.3	6.6	6.1	5.7	6.0	6.5	5.7	6.6
PPS	18.5	19.5	19.4	17.7	19.1	20.3	17.5	19.0	18.7	18.6	18.5	17.5	20.3
PAS	7.9	6.7	5.8	5.1	7.0	5.3	6.7	7.3	5.4	7.7	7.6	5.1	7.9
ACS	5.2	5.8	5.4	5.8	5.4	6.0	5.7	6.4	5.9	5.3	5.6	5.2	6.4
EYL	2.0	1.5	1.4	1.5	1.3	1.2	1.2	1.2	1.1	1.0	0.9	0.9	2.0
EYH	1.7	1.3	1.4	1.4	1.2	1.1	1.2	1.2	1.0	1.0	0.9	0.9	1.7
INO	10.3	10.0	10.9	10.3	10.0	9.6	9.5	9.5	9.7	9.0	9.0	9.0	10.9
NOW	2.2	2.0	1.9	2.0	2.1	2.0	1.9	1.9	1.9	1.8	1.6	1.6	2.2
INW	4.6	4.4	4.4	4.6	4.1	4.4	4.3	4.1	4.3	3.9	3.9	3.9	4.6
ANF	0.1	0.5	0.7	0.4	0.8	0.6	0.6	0.7	0.7	0.5	0.5	0.1	0.8
MOL	5.0	5.0	5.6	5.1	5.0	4.8	4.9	4.7	5.1	4.5	4.6	4.5	5.6
MOW	8.8	9.5	9.4	9.6	9.2	8.9	8.5	8.4	9.2	8.1	8.2	8.1	9.6
ULA	0.5	0.6	0.5	0.4	0.5	0.5	0.5	0.4	0.4	0.5	0.5	0.4	0.6
LLA	0.6	0.5	0.8	0.5	0.6	0.4	0.6	0.5	0.5	0.5	0.5	0.4	0.8
GS1	2.9	3.0	3.5	3.2	2.8	3.4	3.1	3.1	3.6	3.1	3.5	2.8	3.6
GS3	2.8	3.1	3.1	3.3	3.2	3.2	3.8	3.2	3.9	3.1	3.3	2.8	3.9
GS5	2.3	2.2	2.6	2.8	2.7	2.6	2.8	3.2	2.9	2.5	2.4	2.2	3.2
HDH	9.9	10.4	11.6	12.8	10.5	11.9	11.6	11.0	12.2	11.4	11.5	9.9	12.8
TRH	11.4	11.1	13.3	14.2	13.2	13.6	12.7	11.9	12.9	12.6	13.3	11.1	14.2
TAH	8.3	8.9	8.5	9.2	8.4	9.4	9.4	8.4	9.8	8.4	9.2	8.3	9.8
CPH	4.1	4.2	4.4	4.1	4.0	4.3	4.3	3.9	4.2	4.0	4.0	3.9	4.4
HDW	10.4	12.0	11.5	12.8	12.7	12.7	12.4	12.6	12.8	12.0	12.1	10.4	12.8
TRW	8.8	11.0	9.8	12.2	12.3	11.9	11.5	13.1	13.2	12.0	12.1	8.8	13.2
TAW	6.4	6.5	6.3	8.0	7.3	8.1	7.9	8.0	8.3	8.0	7.8	6.3	8.3
CPW	3.4	3.2	2.7	3.2	3.4	3.3	3.9	3.5	3.7	3.0	2.8	2.7	3.9
P1L	12.7	12.4	12.9	13.3	–	14.4	13.1	13.4	14.0	13.7	12.6	12.4	14.4
P1A	14.5	14.4	15.1	15.6	–	17.5	15.2	16.3	17.4	17.0	15.8	14.4	17.5
P1B	6.5	6.7	6.4	7.0	7.2	7.6	6.3	6.9	7.1	6.9	6.6	6.3	7.6

Table 1. cont'd.

	CSIRO H 6662–02	RMNH 4293	RMNH 4292	CSIRO H 7083–01	CSIRO H 6137–07	IPPS 28404–11	IPPS HBO1	IPPS WWPLAL#7	IPPS WWPLAL#8	IPPS 08–19	IPPS 08–18	Min.	Max.
P1H	12.7	13.1	15.6	14.2	–	15.1	13.8	15.1	16.2	16.2	15.4	12.7	16.2
P1I	7.0	6.7	8.0	7.2	–	8.0	6.9	6.7	7.3	7.3	6.6	6.6	8.0
P1P	11.3	11.0	13.9	13.6	–	15.5	12.8	14.3	16.6	15.8	14.9	11.0	16.6
P2L	10.0	9.5	10.3	10.5	10.7	11.7	10.6	11.2	11.5	10.5	10.2	9.5	11.7
P2A	7.7	7.6	7.9	7.7	8.3	8.8	7.4	8.6	9.3	8.3	7.7	7.4	9.3
P2B	6.3	6.1	5.0	5.7	6.6	6.6	5.8	6.7	6.8	6.0	6.2	5.0	6.8
P2H	5.4	5.7	6.6	7.7	5.6	7.7	7.1	8.3	8.7	7.9	7.2	5.4	8.7
P2I	4.2	4.5	5.2	4.8	4.6	5.2	4.7	4.8	4.8	4.9	5.2	4.2	5.2
P2P	6.4	6.3	7.0	8.0	8.1	8.5	7.8	8.6	9.2	7.4	7.8	6.3	9.2
CLO	–	–	–	–	–	–	–	–	–	7.3	6.6	6.6	7.3
CLI	–	–	–	–	–	–	–	–	–	11.0	10.6	10.6	11.0
CLB	–	–	–	–	–	–	–	–	–	1.5	1.5	1.5	1.5
D1L	16.0	14.9	15.0	15.7	–	17.1	16.5	15.3	16.8	15.9	15.9	14.9	17.1
D1A	12.0	11.4	11.9	12.4	–	13.3	12.6	12.2	13.6	13.0	13.3	11.4	13.6
D1B	11.4	11.0	10.6	11.3	10.7	11.7	12.1	10.2	11.7	11.3	11.2	10.2	12.1
D1H	5.8	5.6	7.4	7.0	–	7.3	7.0	7.4	8.1	7.4	6.7	5.6	8.1
D1I	4.6	4.1	4.5	4.7	–	5.4	4.4	5.5	5.3	4.8	4.8	4.1	5.5
D1P	6.9	7.4	8.3	8.4	–	9.0	8.4	8.2	8.8	8.9	8.1	6.9	9.0
D2L	12.8	11.8	14.0	12.9	13.7	14.3	13.5	13.3	13.9	12.8	12.2	11.8	14.3
D2A	9.9	10.0	12.0	10.1	10.6	11.2	10.7	10.5	10.9	9.9	9.7	9.7	12.0
D2B	9.0	9.1	10.2	8.9	9.7	9.8	9.7	9.3	9.4	9.0	9.0	8.9	10.2
D2H	4.9	4.8	6.5	6.0	6.7	6.5	6.0	6.4	7.3	6.1	6.2	4.8	7.3
D2I	3.8	2.9	4.2	4.1	4.0	4.6	3.8	4.3	4.4	3.8	3.4	2.9	4.6
D2P	6.2	6.1	7.6	7.6	8.2	8.0	7.2	7.2	8.6	7.9	7.3	6.1	8.6
ANL	11.0	11.1	12.1	12.6	12.0	12.8	11.5	12.8	12.5	10.9	10.7	10.7	12.8
ANA	7.8	8.4	9.2	8.7	9.2	9.6	8.5	9.7	9.9	8.2	8.1	7.8	9.9
ANB	7.1	7.9	8.7	8.7	8.0	8.3	7.7	8.1	8.4	7.5	7.6	7.1	8.7
ANH	4.0	3.8	4.6	4.8	5.2	5.1	4.3	5.4	5.6	4.8	4.4	3.8	5.6
ANI	3.6	3.3	3.8	4.1	4.1	4.6	3.9	4.6	4.2	4.0	3.5	3.3	4.6
ANP	6.5	5.9	6.0	6.0	6.9	5.8	6.0	6.6	6.7	5.5	6.0	5.5	6.9
CDM	24.2	23.8	24.5	24.6	25.2	24.8	24.7	25.0	25.6	25.4	24.5	23.8	25.6
CPV	11.1	10.3	11.3	10.7	–	11.3	10.0	11.2	11.4	10.5	10.7	10.0	11.4
CPL	2.9	2.6	3.3	3.4	–	3.8	3.9	3.8	4.0	4.3	4.4	2.6	4.4
CPU	11.7	12.2	12.5	12.2	–	13.1	11.6	12.5	12.3	12.9	13.6	11.6	13.6
CFW	6.3	6.3	7.6	6.7	–	7.2	6.9	7.3	7.3	6.9	6.7	6.3	7.6
CFL	9.6	8.9	9.5	9.6	–	9.5	8.5	9.4	9.5	8.2	8.1	8.1	9.6
CST	3.3	3.3	3.6	3.9	3.8	3.3	3.3	3.4	3.4	3.2	3.1	3.1	3.9
CTR	5.0	5.0	5.5	6.2	7.3	6.6	6.2	5.3	7.2	6.9	6.0	5.0	7.3
CTL	6.8	6.9	7.0	7.5	8.1	7.7	7.2	7.1	7.8	8.0	7.4	6.8	8.1
DAO	0.6	0.6	0.5	1.8	0.5	1.0	0.7	1.4	1.2	0.5	1.6	0.5	1.8
DAI	1.6	1.5	1.9	1.5	1.2	1.6	0.8	1.6	1.6	1.0	1.6	0.8	1.9
DPI	8.7	10.0	8.7	9.4	10.2	9.5	8.0	10.4	9.5	9.5	8.3	8.0	10.4
DPO	10.1	8.7	9.4	9.4	9.5	10.0	9.4	9.2	9.7	8.8	9.4	8.7	10.1
PDI	7.2	6.1	7.4	7.5	8.1	7.9	7.2	6.7	7.1	6.6	7.4	6.1	8.1
PDO	11.3	10.2	8.5	10.2	9.3	10.0	10.7	10.9	9.6	11.4	10.8	8.5	11.4

(occasionally 3) prominent longitudinal ridges (medial ridge much stronger and more pronounced) that extend entire length of crown onto cusps; medial cusp short but strong, much shorter than rest of crown, flanked by two pairs of slightly shorter lateral cusps, outer pair much shorter.

Pectoral fins large, broadly triangular, very weakly falcate; anterior margin weakly convex, apex narrowly rounded; posterior margin shallowly concave; free rear tip broadly rounded, inner margin convex; base broad 48–54% of fin length; length from origin to rear tip 1.20–1.34 times in anterior margin length; much more than twice area of first dorsal fin; origin about under third gill slit; fin apex about opposite free rear tip when fin is elevated and adpressed to body.

Pelvic fins broadly triangular and not falcate; length of anterior margin 0.58–0.71 of pectoral-fin anterior margin; area about 1.5 times that of anal fin; anterior margin nearly straight and slightly concave near base; apex moderately rounded to subangular; posterior margin nearly straight; free rear tip moderately rounded, inner margin nearly straight; posterior margin, rear tip and inner margin forming a broad triangle with an ~60° apex. Claspers of adult male (IPPS 08–18, 1282 mm TL) moderately short and stout, relatively broad, not tapering sharply distally, outer length 6.6–7.3% TL, base width 22.0–22.8% of outer length; clasper glans extending to about a third of clasper outer length.

First dorsal fin relatively small, low, raked, subtriangular, not falcate; angle of apex about ~90°; anterior margin nearly straight, slightly concave basally; apex angular; posterior margin nearly straight to very shallowly concave; free rear tip pointed, inner margin slightly concave; origin over posterior half of pectoral-fin inner margin, midpoint of base 0.87–1.17 times closer to pectoral insertions than pelvic origins; anterior margin sloping strongly posterodorsally from its base; free rear tip just anterior to over pelvic-fin origin; posterior margin arcing strongly posteroventrally from apex at an angle of ~45°; insertion just posterior to level of dorsal-fin apex. First dorsal fin base 1.49–1.81 in interdorsal space, 2.04–2.44 in dorsal caudal margin; height 1.38–1.97 in base; inner margin 1.26–1.64 in height, 1.85–2.74 in base.

Second dorsal fin large, apically narrow, subtriangular; almost as tall as first dorsal fin, height 0.83–0.93 times first dorsal-fin height, base 0.79–0.96 times first dorsal-fin base; anterior margin weakly concave basally, slightly convex distally; apex moderately rounded; posterior margin convex distally and basally concave; free rear tip acutely pointed, inner margin slightly concave; origin behind pelvic-fin free rear tips; rear tip slightly behind anal-fin free rear tip, in front of upper caudal-fin origin by 0.29–0.98 times its inner margin; posterior margin curving posteroventrally from apex; insertion slightly

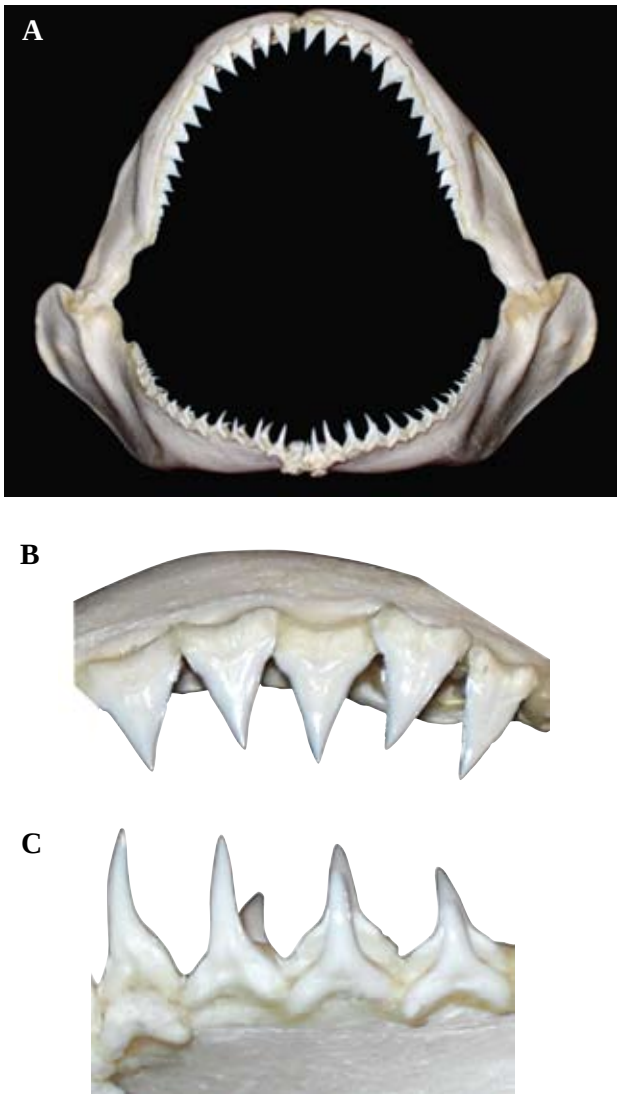

Figure 4. Jaw (A), upper anterior (B) and lower anterior (C) teeth of *Lamiopsis tephrodes* (PMH 293–3, male 1280 mm TL).

Figure 3. Upper precaudal pit of an adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL, fresh). Arrow indicates the shallow, longitudinal precaudal pit.

behind fin apex. Second dorsal-fin base 0.55–0.72 in dorsal–caudal space; height 1.30–1.88 in base; inner margin 0.55–0.78 in height, 2.12–3.08 in base.

Anal fin apically narrow and semi-falcate; height 0.70–0.85 times second dorsal-fin height, base length 0.78–0.98 times second dorsal-fin base; anterior margin indented basally and slightly convex distally; apex subangular; posterior margin notched at much greater than a right angle; free rear tip acutely pointed, inner margin nearly straight; origin almost opposite second dorsal-fin origin; insertion slightly anterior to second dorsal-fin insertion, slightly posterior to anal-fin apex; free rear tip in front of lower caudal-fin origin by about a third of its inner margin length; posterior margin slanting slightly posterodorsally and then abruptly posterodorsally. Anal-fin base expanded anteriorly as very short preanal ridges (obscure), less than a quarter length of rest of base. Anal-fin base 0.62–0.79 in anal–caudal space; height 1.49–2.10 in base; inner margin 0.74–0.90 in height, 1.77–2.41 in base.

Caudal fin narrow-lobed and asymmetrical, with short terminal lobe and prominent, long, narrowly expanded, weakly falcate ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave just anterior to subterminal notch, with prominent lateral undulations; preventral margin moderately convex, tip of ventral caudal-fin lobe subangular; lower postventral margin nearly straight; upper postventral margin nearly straight except for convex section at subterminal notch; notch between postventral margins deep; subterminal notch a narrow, deep slot; subterminal margin slightly concave to almost straight, terminal margin irregular and deeply concave, lobe formed by these margins angular, tip of tail narrowly rounded. Length of dorsal caudal margin 2.90–3.22 in precaudal length, preventral caudal margin 2.16–2.48 in dorsal caudal margin, terminal lobe

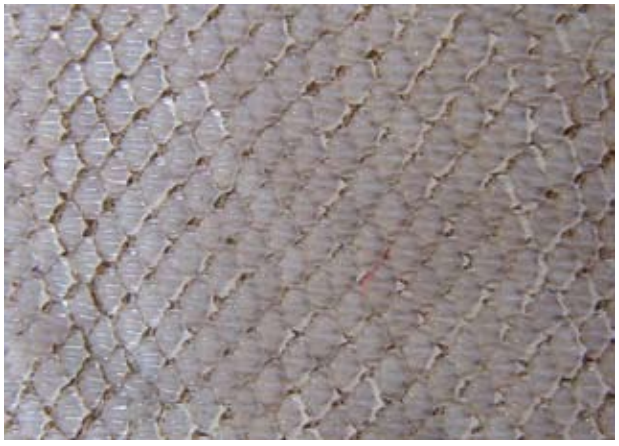

Figure 5. Cusps of the flank denticles of *Lamiopsis tephrodes* (IPPS 08–18, adult male 1282 mm TL, preserved).

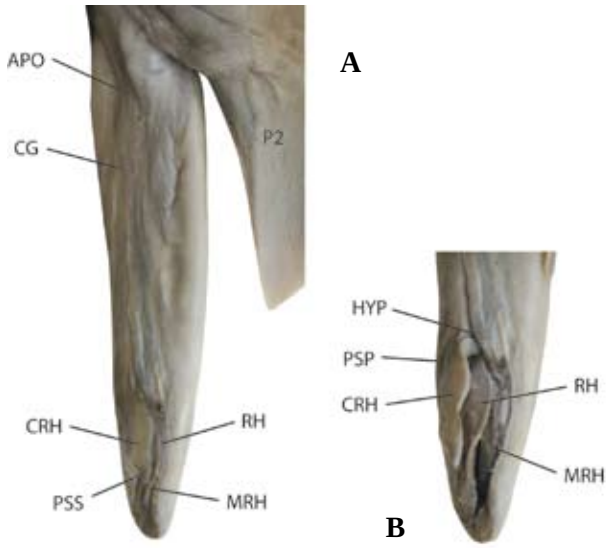

Figure 6. Clasper (left) of an adult male *Lamiopsis tephrodes* (IPPS 08–18, 1282 mm TL): A. glans not dilated; B. glans spread. APO, apopyle; CG, clasper groove; CRH, cover rhipidion; HYP, hypopyle; MRH, mesorhipidion; P2, pelvic fin; PSP, pseudopera; PSS, pseudosiphon; RH, rhipidion.

from caudal tip to subterminal notch about 3.09–3.55 in dorsal caudal margin, subterminal margin length 1.49–2.15 in terminal margin.

Counts of total vertebral centra (TC, n=4) 174–181, precaudal centra (PC) 98–100, monospondylous precaudal (MP) centra 50–51, diplospondylous precaudal (DP) centra 48–49, diplospondylous caudal (DC) centra 75–81; MP centra 27.9–28.7%, DP centra 26.8–28.2%, and DC centra 43.1–45.3% of TC centra. Ratios of DP/MP centra 0.96–0.98, DC/MP centra 1.50–1.62.

COLORATION.— When fresh: dorsal surface of head, trunk and tail slate-grey, graduating to white ventrally on midlateral surface. Demarcation of light and dark surfaces (waterline) of head strong, extending along lateral angle of the snout anteriorly to level of nostrils, then extending dorsoposteriorly towards upper margin of eye; from posterior eye extending from upper margin to midpoint of first gill opening, diffuse over mid-level of 3rd gill opening, elevated along upper ends of 4th and 5th openings (most of membranes of 4th and 5th openings whitish); a narrow dark area extending around ventral margin of eye, not visible ventrally; waterline irregular, jagged along abdomen to origin of pelvic fin; waterline directed posterodorsally above pelvic-fin base, diffuse, extending along tail mid-laterally; pale area continuing onto base of caudal fin, barely apparent as a pale marking along upper lobe to origin of the terminal lobe. Dorsal fins similar in colour. First dorsal fin bi-tonal, dark anterior margin with broad slate-grey posterior margin

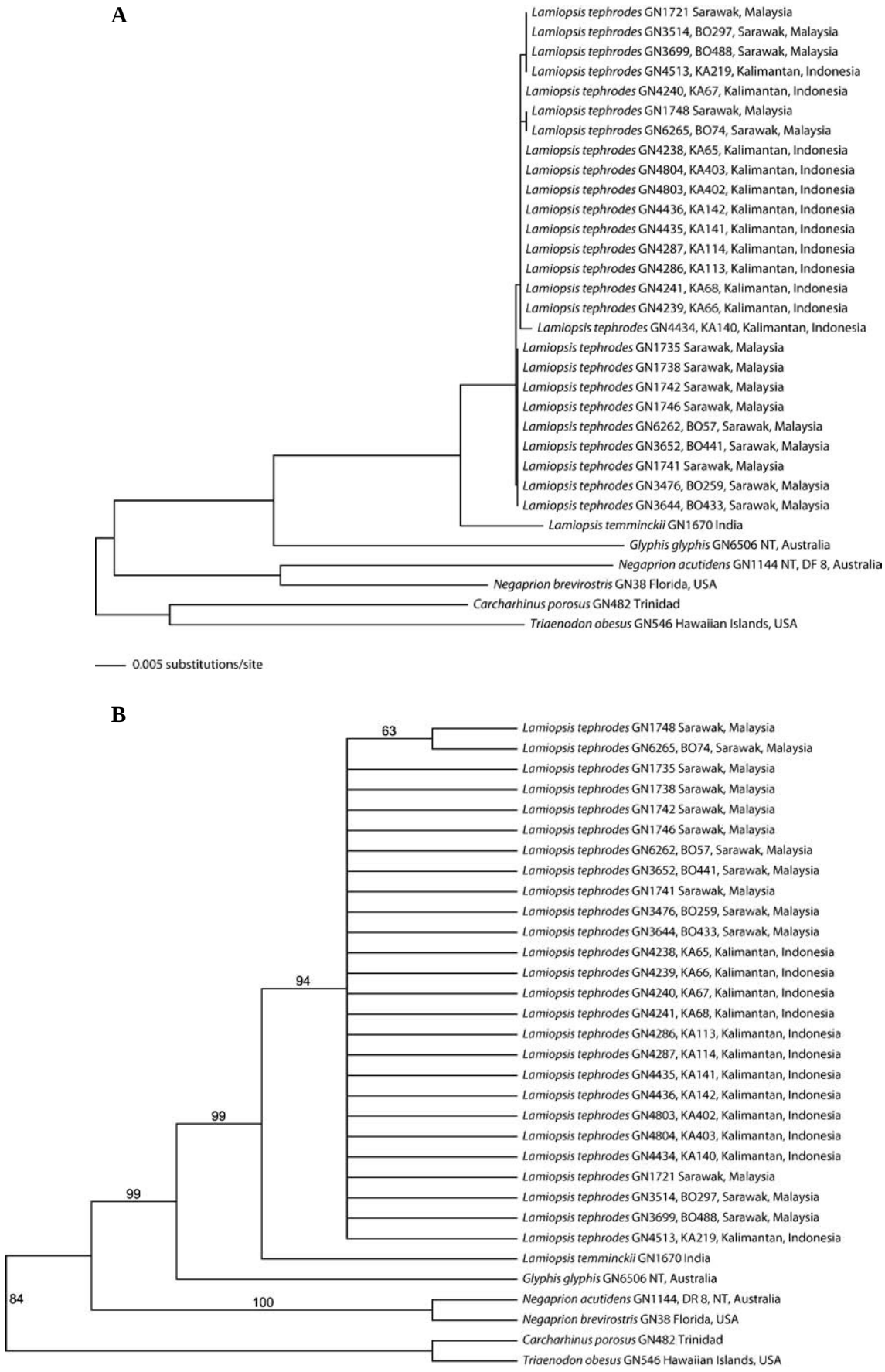

Figure 7. (A) Neighbour-Joining tree based on K2P distance, (B) Parsimony Bootstrap with 1000 replicates and (C) Maximum Likelihood tree using a GTR+I+Γ model (General Time Reversible + Invariant sites + gamma distributed rates). Model parameter values were optimized recursively for the Likelihood analysis as the search progressed.

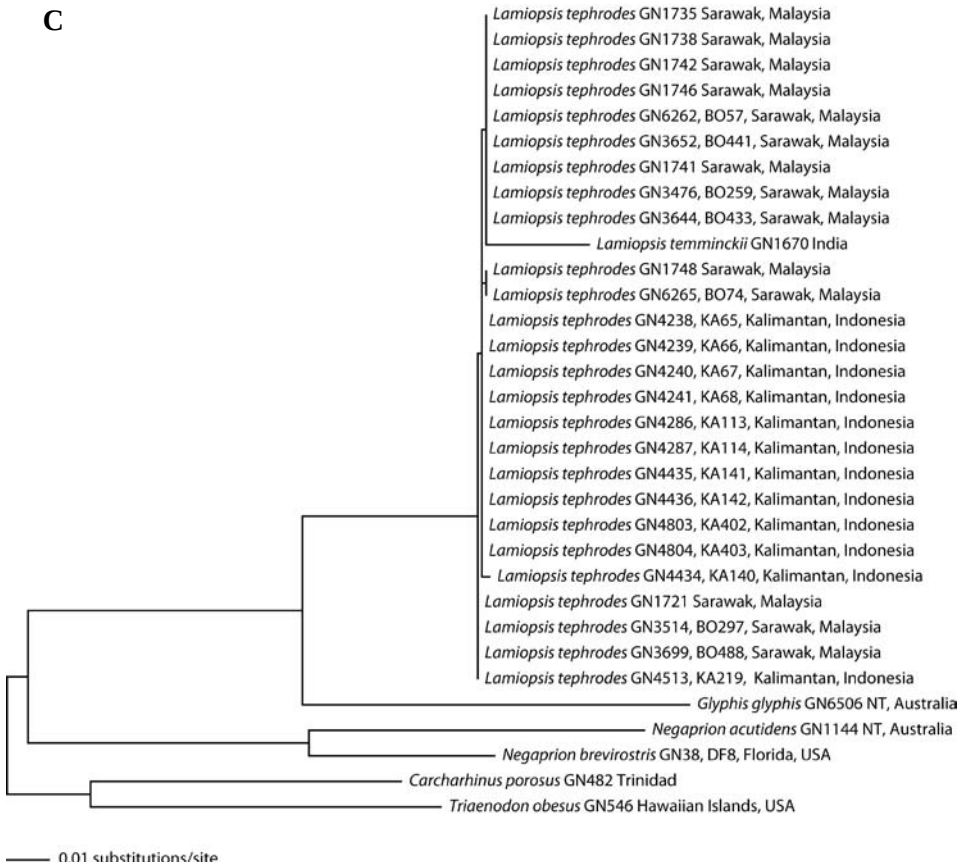

Figure 7. cont'd.

and fin base; central portion of fin for more than half its height pale off-whitish, patch extending posteriorly and converging towards fin insertion; inner margin whitish. Second dorsal fin with a posterior dark marginal band, similar in width to that of first dorsal fin; pale anterior margin distinctly smaller than that of first; inner margin whitish. Anal fin mostly pale, posterior half dusky. Caudal fin dusky, paler medially; anterior margin narrowly black-edged; terminal lobe with broad greyish marking (similar to those of dorsal fins); similar dark marking extending along postventral margin to ventral lobe apex. Pectoral fins not uniform on both surfaces; upper surface slate grey basally, grading rapidly to paler, almost whitish posterior and inner margin (more distinct in larger fixed specimens), basal third of anterior margin narrowly whitish; naked insertion with a blackish and white membrane; ventral surface uniformly white. Pelvic fins similar to pectoral fins except basal portion of fin whitish rather than dark; whitish ventrally (largest fixed specimens dusky distally). Claspers white (adult males with some dusky areas on dorsal surface of claspers). Eyes silvery yellow with a black pupil; nictitating membrane translucent.

SIZE.— Whole specimens examined ranged in length from 408–1282 mm TL. Three males of 408–789 mm TL were juveniles, one male of 1080 mm TL was a subadult (claspers almost fully calcified), and one male was fully mature at 1282 mm TL. The smallest specimen (408 mm TL) had an umbilical scar indicating that it is close to the size at birth. Additional specimens collected in Borneo, but not retained, included a mature female of 1450 mm TL and two subadult males of 1050 and 1060 mm TL. Maximum sizes for males and females is poorly defined as published information is combined with data for *L. temminckii* from Indian waters.

DISTRIBUTION.— Specimens examined in this study were mostly collected from off Borneo, with the three of the four jaws examined from Penang (Malaysia) and one from Phuket (Thailand). The two Indonesian specimens collected from Jakarta were from fishers operating off southern Kalimantan and should not be considered as from Java. The extent of occurrence of this species is poorly defined. Possibly also occurs off southern China and more widespread in the Indo–Malay Archipelago but validated records need to be obtained.

DISCUSSION

Although the holotype of *Lamiopsis tephrodes* was not examined, there is no doubt that the specimen described and illustrated by Fowler (1905) belongs to the genus *Lamiopsis*. As previously mentioned, the smaller paratype

Figure 8. Lateral view of lectotype of *Lamiopsis temminckii* (BMNH 1862.8.16.11, juvenile male 1057 mm TL).

described by Fowler (1905) is referrable to *Carcharhinus* sp. A [*sensu* Compagno *et al*., 2005] and not *Lamiopsis tephrodes*.

Following examination of the dried syntype of *L. temminckii* in the BMNH collection (BMNH 1862.8.16.11) and comparison with the measurements in the original description by Müller & Henle (1839), it is apparent that this is the specimen on which Müller & Henle based their description. Their illustration of the species lacks claspers so it may be of a different specimen or a composite. We herein designate the dried specimen BMNH 1851.8.16.11 as the lectotype for *L. temminckii*. A further syntype of *L. temminckii* listed as being deposited in the Paris museum (MNHN) was not found during a visit by the senior author (WW) in November 2009 and curatorial staff noted that there was no record of this specimen on their database. Another syntype of this species deposited at RMNH was also not encountered during the same trip. If these other syntypes are located and belong to *Lamiopsis*, these should be recognised as paralectotypes for this species.

Comparisons of the morphology of *Lamiopsis tephrodes* with *L. temminckii* was limited to the dried lectotype of the latter species (Fig. 8) and a number of measurements in the original Müller & Henle description (converted to mm using conversions of the German Fuss, Zoll and Linie measurements originally used). Only a subset of characters could be measured on the lectotype. Most of the morphometrics taken fell within, or close to, the ranges for the same character taken for *L. tephrodes*, but several characters differed markedly in the dried lectotype. The main differences between the dried lectotype of *L. temminckii* and the 11 specimens of *L. tephrodes* were: more posteriorly positioned dorsal fins (pre-first dorsal length 35.5 vs. 31.4–33.3% TL, pre-second dorsal length 66.3 vs. 59.5–61.8% TL), preanal length (66.5 vs. 58.4–61.0% TL), shorter dorsal fin bases (first dorsal-fin base 9.3 vs. 10.2–12.1% TL, second dorsal-fin base 7.7 vs. 8.9–10.2% TL), shorter caudal fin (dorsal caudal margin 21.4 vs. 23.8–25.6% TL). Although the differences listed

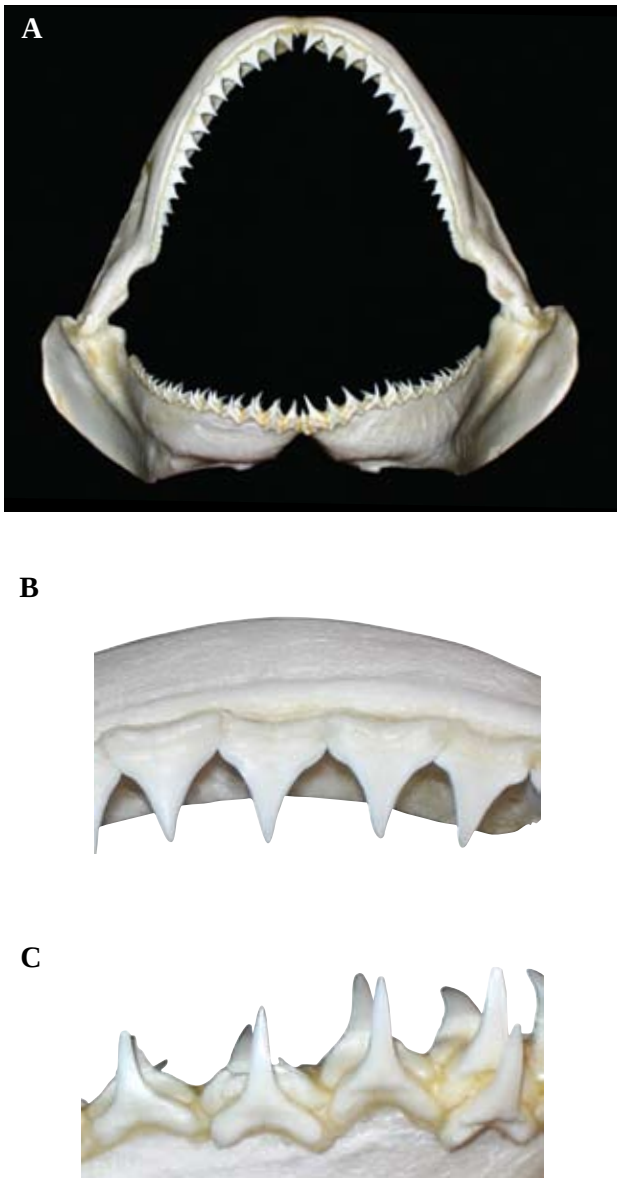

Figure 9. Jaw (A), upper anterior (B) and lower anterior (C) teeth of *Lamiopsis temminckii* (PMH 201–2, female 1475 mm TL).

Table 2. Differences between the dentition of *Lamiopsis tephrodes* and *Lamiopsis temminckii*.

Lamiopsis tephrodes	*Lamiopsis temminckii*
Upper teeth triangular in shape, both margins symmetrical. Distal and mesial shoulders mildly pronounced	Upper teeth more cordiform in shape, tapering just below basal ledge. Distal mesial shoulders very pronounced
Posterior molariform teeth in upper jaw relatively few. Generally 3–5 rows	Posterior molariform teeth in upper jaw more numerous in count. Generally 5–7 rows
Upper lateral and posterior teeth noticeably oblique with convex mesial margins	Upper lateral and posterior teeth relatively straight with mesial margins slightly angular but rarely convex
Serrations on upper teeth usually coarser basally on shoulders, descending to much finer serrations towards apex	Serrations more evenly distributed, and not noticeably coarser basally
Serrations generally coarse in upper teeth of adults	Serrations generally finer in upper teeth of adults
Lower teeth sometimes with very finely serrated cutting edges in adults	Lower teeth with entirely smooth cutting edge
Slightly fewer tooth rows, 33–40/34–40	Slightly more tooth rows, 42–44/40–43

above are significant, they could be due to the specimen of *L. temminckii* being a dried and stuffed specimen. For example, using approximate measurements from the illustration of *L. temminckii* in Müller & Henle, estimates of 33.8 and 62.3% TL are obtained for pre-first dorsal and pre-second dorsal lengths, respectively. Although these are still greater than the ranges for *L. tephrodes*, they are relatively similar. Furthermore, from the original description, the measurements of the dorsal-fin bases are shorter in *L. temminckii* compared to *L. tephrodes*, i.e. first dorsal-fin base 2.9 vs. 2.0–2.4 in dorsal caudal margin, second dorsal-fin base 4.0 vs. 2.4–2.8 in dorsal caudal margin.

All three of the molecular analyses (Fig. 7) show identical interrelationships between *Lamiopsis* and the outgroup taxa. All three analyses also indicate that *Lamiopsis tephrodes* is distinct from *Lamiopsis temminckii* at this locus. However, the parsimony and the neighbour-joining analyses of the data suggest that *L. temminckii* is the sister taxon to a monophyletic *L. tephrodes*. The Maximum Likelihood (ML) analysis, by contrast, suggests that *L. temminckii* arose and differentiated as a lineage from within *L. tephrodes*. Distinguishing between these two alternative scenarios must await collection and analysis of sequence data from nuclear markers. While the molecular data suggests that the Indian form *L. temminckii* is distinct from the South-east Asian form *L. tephrodes*, we caution that the inference is based on a single mitochondrial marker (ND2). The inference is thus the tree topology for that particular gene. Gene trees do not always correspond to the species trees that contain them. This is because gene tree lineages coalesce at rates that are affected by the mutation rate, the effective population size and the migration rate; parameters that often vary between genes. In order to deduce robust species trees from gene trees it is important to base inferences from a suite of independent genetic markers from both the nucleus and the mitochondrial genomes. This said, there is generally a reasonably close correspondence between broad patterns of diversification assessed by mitochondrial markers and species differentiation.

Additional, preserved or fresh material of *L. temminckii* is required to investigate whether these differences are accurate and to determine what other differences there may be. *Lamiopsis temminckii* possibly attains a larger size, or at least matures at a larger size than *L. tephrodes*. The lectotype of *L. temminckii* is a juvenile male of 1057 mm TL with very little development of the claspers, whilst a specimen of *L. tephrodes* at 1080 mm TL had well-developed, almost fully calcified claspers. More specimens are required to determine whether such size differences are real.

Certain diverse aspects of the dental morphology of this species as compared to *Lamiopsis temminckii* have been noted and are discussed here (see Figs 4 and 9). Although noticeable, these interspecific differences are only mildly consistent and may vary to some extent, particularly when taking into account the small number of positively identified specimens of *Lamiopsis tephrodes* for which the dental characters have been noted. The primary characters separating these two species are outlined in Table 2.

Lamiopsis temminckii is listed as Endangered in the IUCN *Red List of Threatened Animals* based on its distribution in heavily exploited regions and its apparent rarity (White *et al*., 2008). Given the resurrection of *Lamiopsis tephrodes* from Borneo, this assessment needs to be revised and a separate assessment established for

L. temminckii. The absence of this genus from Indonesian waters, other than off Kalimantan, during extensive surveys of fish landing sites over the last 10 years, indicates that localised depletions have likely occurred (White *et al*., 2006). Both species occur in shallow areas, often near large river outflows, in regions with heavy exploitation levels. Thus, both are likely to be of conservation concern and threatened in their respective regions.

Comparative material

Lamiopsis temminckii: 8 specimens: BMNH 1851.8.16.11 (lectotype, dried and stuffed), juvenile male 1057 mm TL, India; PMH 201–1 (jaw only), male 1440 mm TL, PMH 201–2 (jaw only), female 1475 mm TL, PMH 201–3 (jaw only), male 1490 mm TL, PMH 201–4 (jaw only), female 1517 mm TL, PMH 201–5 (jaw only), female 1530 mm TL, PMH 201–6 (jaw only), female 1563 mm TL, Baleshwar, India; PMH 201–7 (jaw only), unsexed ~1450–1500 mm TL, Chittagong, Bangladesh.

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Scoliodon macrorhynchos (Bleeker, 1852), a second species of spadenose shark from the Western Pacific (Carcharhiniformes: Carcharhinidae)

William T. White[1], Peter R. Last[1] & Gavin J.P. Naylor[2]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Florida State University, School of Computational Science/Department of Biological Science, Tallahassee, FL 32304, USA

ABSTRACT.— The genus *Scoliodon*, represented by a widespread Indo-Pacific species *S. laticaudus*, was previously considered to be monotypic. Recent molecular analyses of *Scoliodon* from across its geographic range have shown that three species should be recognised: one from the coastal waters of India, Pakistan and Sri Lanka, one from the Western Central Pacific, and a third species from the Bay of Bengal, off western Thailand. *Scoliodon macrorhynchos* (Bleeker, 1852), which was described from Batavia (=Jakarta, Indonesia), is resurrected from the junior synonymy of *S. laticaudus*. As the whereabouts of the holotype of *S. macrorhynchos* appears to be unknown and is possibly lost, we provide a redescription of this species based on three of Bleeker's specimens and recently collected material from the Western Central Pacific. Although *S. macrorhynchus* is morphologically similar to *S. laticaudus*, it differs in some morphological characters and exhibits substantial DNA sequence divergence in the mitochondrial marker NADH2. A third species from off western Thailand requires further investigation to determine its distribution in the Bay of Bengal and conspecificity with *S. muelleri*, originally described from 'Bengale' by Müller & Henle.

Key words: *Scoliodon laticaudus* – *Scoliodon macrorhynchos* – Western Central Pacific – resurrection – redescription – sequence divergence

PDF contact: william.white@csiro.au

INTRODUCTION

The genus *Scoliodon* was proposed by Müller & Henle (1837), with *Scoliodon laticaudus* Müller & Henle, 1838 the type species by subsequent monotypy (Müller & Henle, 1838). This genus belongs to the subfamily Scoliodontinae Whitley, 1934, being distinguished from the Carcharhininae and Galeocerdinae by clasper and cranial morphology and a very shallowly concave postventral caudal margin (Compagno, 1988). The genus *Scoliodon* is considered to be the closest relative of hammerhead sharks (Sphyrnidae) and contains one of the smallest carcharhinid species at ~74 cm maximum total length (Compagno, 1988). Members of this genus are closest to members of *Rhizoprionodon* and *Loxodon* but, in addition to the characters above for the subfamily, differ from these genera in their greatly depressed and trowel-shaped snout, more compressed and taller caudal peduncle, broader and more triangular pectoral fins, and more posteriorly located first dorsal fin.

The genus *Scoliodon* has a very complicated nomenclatural history with early studies (e.g. Garman, 1913; Fowler, 1941) having it confused with members of *Loxodon* and *Rhizoprionodon*. The nomenclature of these genera was resolved by Springer's (1964) revision in which he recognised and distinguished *Rhizoprionodon* with 7 species, and *Scoliodon* and *Loxodon* as monotypic. *Scoliodon laticaudus* was described by Müller & Henle (1838) from India, and until the last decade or so has been considered the sole member of the genus, with an Indo–West Pacific distribution, from northeast Africa to southern Japan (Compagno *et al.*, 2005). In the same publication as the *S. laticaudus* description, but dated the following year, Müller & Henle (1839) also described *Carcharias* (*Physodon*) *muelleri* from Bengal, but although considered to be a valid species by some authors (e.g. Garman, 1913; Fowler, 1941), it has been widely regarded as a synonym of *S. laticaudus* (Compagno, 1984).

The historical confusion over the specific names *sorrakowah* and *palasorra*, which at times were both applied to *S. laticaudus*, was also resolved by Springer (1964). The authority for *Carcharias palasorra* is now considered to be Bleeker (1854), based on the vernacular name of "Pala Sorra" given by Russell (1803) for the

species from Coromandel in India, and is now considered a junior synonym of *S. laticaudus* (Springer, 1964). Although Cuvier (1829) has been considered the authority for *C. sorrakowah* (including Eschmeyer, 2010), Cuvier only made a footnote about Russell's '*sorrakowah*' in reference to the native names used by Russell. He did not use the generic name (*Sq.*) before this name, as he normally did, implying that he did not intend to name the species. Therefore, the authority for *Carcharias sorrakowah*, based on Russell's (1803) name of "Sorra Kowah", should be recognised as Bleeker (1854). The identity of this species is doubtful and unlikely to be resolved with Russell's figure indicating that it is either *Rhizoprionodon acutus* or *R. oligolinx*, but no types are available to confirm this with certainty (Springer, 1964).

In 1852, Bleeker described *Carcharias* (*Scoliodon*) *macrorhynchos* from Jakarta in Indonesia, but the species was later synonomised with *S. laticaudus* by Günther (1870), and in an unpublished manuscript, Bleeker accepted this as correct (Springer, 1964). However, recent surveys throughout South-east Asia have enabled more detailed taxonomic and molecular comparisons of specimens from this genus throughout its range. The present account re-examines the South-east Asian species of *Scoliodon*, resurrects *S. macrorhynchos* as a valid species and provides a detailed redescription of this species.

METHODS

Measurement terminology follows Compagno (1984, 1988, 2001) who assigned names and abbreviations to measurements often indicated by descriptive phrases (example: snout to upper caudal origin = precaudal length = PRC). Dentitional terms generally follow Compagno (1979, 1988, 2001). Vertebral terminology, method of counting and vertebral ratios follow Springer & Garrick (1964) and Compagno (1979, 1988, 2001).

A total of 21 specimens of *Scoliodon macrorhynchos*, 7 specimens of *S. laticaudus*, and the holotype of *S. muelleri* were measured in full (Table 1). In the descriptive section, morphometric and meristic values of *S. macrorhynchos* are expressed as ranges. Meristics were taken from radiographs of 13 specimens of *S. macrorhynchos*. Counts were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of upper lobe of caudal fin) and caudal (centra of the caudal fin) vertebrae. Tooth row counts were taken in situ or from excised jaws of 8 specimens of *S. macrorhynchos* and 7 specimens of *S. laticaudus*.

Muscle tissue samples were taken from specimens collected in the field and stored in either 95% alcohol or DMSO until processed in the laboratory. Total DNA was extracted from the tissue samples using High Pure PCR Template Preparation Kit (Roche Diagnostics). Extracted total DNA was stored at –20° C. Sub-sets of the extracted template were diluted to 1/10 of original strength and stored for subsequent use in PCR reactions. Samples were PCR amplified using Hot Start Taq (Promega) using primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (Naylor *et al*., 2005). These primers are designed to bind to the ASN and ILE tRNA regions flanking the NADH2 gene in the mitochondrial genome of elasmobranchs. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of T.aq, PCR buffer, 2.5 mM, $MgCl^2$, 1.0 mM of DNTPs, and 1.0 mM of each primer. The reaction cocktail was denaturised at 94˚C for 3 minutes, after which it was subjected to 35 cycles of 94°C /30s, 48°C /30s and 72°C /90s followed by an indefinite hold in the thermal cycler at 4°C.

A sample of the completed PCR reaction was run on 1% agarose gels, stained, visualised and photographed under UV light to assess the success of PCR amplification. Samples with successful amplification products were purified using purification plates (Millipore, MA) attached to a vacuum manifold. The purified PCR products were quantified and diluted to between 30–100 ng/µL and subsequently sent to SeqWright (Houston, Texas) for sequencing. The software packages Phred and Phrap were used to read sequence traces, assign quality values, make base calls and produce output files for subsequent alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment.

The aligned nucleotide sequences were subjected to phylogenetic analysis using PAUP* (v4.0b106). The data were subjected to Neighbour joining based on K2P Distance, Parsimony and Maximum Likelihood analysis using parameter optimised models that best fit the data. The topologies across all methods were consistent with each other.

Specimens are referred to by the following prefixes for their registration numbers: BMNH, British Museum of Natural History, London; IPPS, Institut Penyelidikan Perikanan Sarawak, Kuching, Malaysia; CSIRO, Australian National Fish Collection, Hobart; RMNH, Rikjsmuseum van Natuurlkjke Histoire, Leiden; MNHN, Museum National d'Histoire Naturelle, Paris. In the molecular trees, field codes (prefixed by BO, KA or TW) are provided for samples collected by Drs J. Caira and K. Jensen, and data and images for these specimens are available at http://tapeworms.uconn.edu.

FAMILY CARCHARHINIDAE Jordan & Evermann, 1896

Genus *Scoliodon* Müller & Henle, 1837

Type species. *Scoliodon laticaudus* Müller & Henle, 1838

Species.— *Scoliodon* includes three species: *S. laticaudus* Müller & Henle, 1838, *S. macrorhynchos* (Bleeker, 1852), and a third species which may be undescribed or possibly equates to *S. muelleri* (Müller & Henle, 1839) which was described from Bengal and is presently considered a junior synonym of *S. laticaudus*.

Scoliodon macrorhynchos (Bleeker, 1852)

Figs 1–5, 8; Table 1

Carcharias (Scoliodon) macrorhynchos Bleeker, 1852: 25 (Type locality: Jakarta, Indonesia).
Carcharias (Scoliodon) macrorchynchos: Bleeker, 1852, 7, 9, 27 (Jakarta, Indonesia). Misspelling.
Carcharias (Scoliodon) macrorhijnchos: Bleeker, 1852, pl. 1 (Jakarta, Indonesia). Misspelling.
Carcharias (Scoliodon) macrorhynchus Bleeker, 1858, 435 (Pamangkat, West Borneo). Misspelling.
Cynocephalus (Scoliodon) macrorhynchus: Bleeker, 1879, 2 (China). New combination.
Carcharias laticaudus (non Müller & Henle): Casto de Elera, 1895, 613 (Philippines). Misidentification.
Physodon mülleri: Garman, 1913, 108 (China). Misidentification.
Scoliodon sorrakowah Garman, 1913: 108 (Singapore). Misidentification.
Scoliodon laticaudus (non Müller & Henle): Jordan & Snyder, 1901, 39 (Japan). Misidentification.

Material examined. 23 specimens: BMNH 1867.11.28.190, female 466 mm TL, probably collected with holotype (Jakarta, Indonesia); CSIRO H 4425–01, subadult male 317 mm TL, CSIRO H 4425–02, female 359 mm TL, Kuching, Sarawak, Malaysia, 16 Oct. 1995; CSIRO H 5861–01, adult male 436 mm TL, CSIRO H 5861–05, female ~440 mm TL (tail tip damaged), CSIRO H 5861–06, female 239 mm TL, Muara Baru fish landing site, Jakarta, Indonesia (caught from southern Kalimantan according to fisheries information), 18 Mar. 2002; CSIRO H 6295–21, adult male 458 mm TL, Tashi fish landing site, northeastern Taiwan, 24 May 2005; CSIRO H 7074–01, female 325 mm TL, CSIRO H 7074–02, subadult male 337 mm TL, CSIRO H 7074–03, female 353 mm TL, CSIRO H 7074–04, female 346 mm TL, CSIRO H 7076–01, adult male 562 mm TL, CSIRO H 7076–02, pregnant female 511 mm TL (jaws and chondrocranium only), CSIRO H 7076–03, (2 embryos from CSIRO H 7076–02) females 147 and 148 mm TL, CSIRO H 7076–04, adult male 555 mm TL (jaws and chondrocranium only), CSIRO H 7076–05, female 548 mm TL, Tuen Mun fish market, caught from Pearl River Estuary, Hong Kong, ~22°20′ N, 113°50′ E, 04 Sep. 2009; CSIRO H 6227–01, adult male 387 mm TL, Sarawak, Malaysia, Jun. 2002; IPPS HBO22, adult male 390 mm TL, Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 2002; IPPS WWPLAL#1, adult male 426 mm TL, IPPS WWPLAL#2, female 456 mm TL, IPPS WWPLAL#3, female 396 mm TL, IPPS WWPLAL#4, female 344 mm TL, Kuching fish market, Sarawak, Malaysia, 06 Nov. 2009; RMNH 7369 (2), female 426 mm TL, female 236 mm TL, Jakarta (as Batavia), Indonesia, 1851?.

DIAGNOSIS.— A small carcharhinid (to 71 cm TL) with the following combination of characters: a long and extremely flattened snout; slender body and tail; teeth smooth-edged with slender, strongly oblique, blade-like cusps and no cusplets; anterior teeth strongly sexually dimorphic with those of adult males greatly elongate and flexuous; total tooth row counts 25–28/23–28 rows or 48–56 total rows; second dorsal-fin origin well posterior of anal-fin origin, about opposite posterior third of anal-fin base; second dorsal-fin origin to anal-fin origin 6.0–9.1% TL, 1.3–2.5 times second dorsal-fin base; interdorsal space 17.9–22.2% TL; pelvic fins small, anterior margins 41–56% of pectoral anterior margin; first dorsal fin small, broadly triangular, origin behind pectoral-fin free rear tips, free rear tip over posterior half of pelvic-fin bases, length 12.9–15.5% TL, inner margin 2.1–3.0 in base; second dorsal fin very small, base 2.0–3.5 times height; height 18–27% of first dorsal-fin height; anal fin large, length 11.1–14.1% TL, height 1.7–2.5 times second dorsal-fin height, base 1.9–3.1 times second dorsal-fin base; total vertebral count 149–171, monospondylous precaudal count 44–50, diplospondylous precaudal count 53–64, diplospondylous caudal count 49–59, precaudal count 98–114; colour greenish-bronze dorsally, off white ventrally when fresh; when preserved, slate-grey dorsally, whitish ventrally with waterline clearly demarcated along head, more diffuse along body, no distinct black spots on fins.

DESCRIPTION.— Body slender, compressed, trunk narrowly triangular and almost narrowly pear-shaped in section at first dorsal-fin base; length of trunk from fifth gill slits to vent 0.97–1.28 times head length. Predorsal, interdorsal and postdorsal ridges absent from midline of back; lateral ridges absent from body. Caudal peduncle moderately stout, somewhat compressed, suboval in cross-section at second dorsal-fin insertion; postdorsal and postventral spaces flattened; anal-caudal space with a shallow median groove; lateral surfaces rounded, without keels or ridges; height of caudal peduncle at 2nd dorsal-fin insertion 1.18–2.08 times its width, 1.65–2.17 times in dorsal–caudal space. Precaudal pits present; upper pit a deep, arcuate and crescentic depression; lower pit obvious but reduced, present as a shallow horizontal depression at lower caudal-fin origin.

Head length to fifth gill slit 0.73–0.97 times in pectoral–

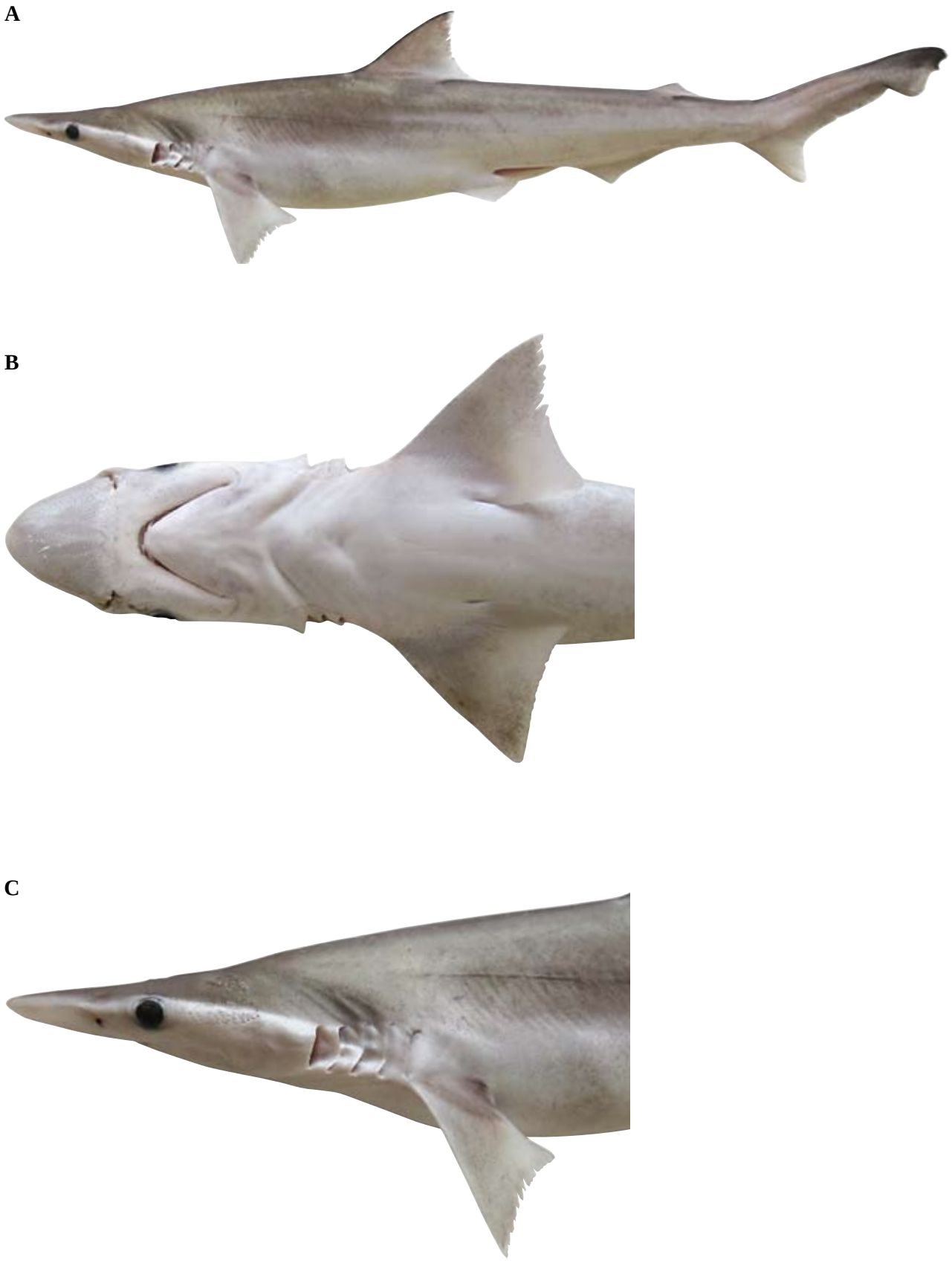

Figure 1. *Scoliodon macrorhynchos* IPPS WWPLAL#1 (adult male 426 mm TL, fresh): A. lateral view; B. ventral view of trunk; C. lateral view of trunk.

Figure 2. Lateral view of *Scoliodon macrorhynchos* CSIRO H 7074–01 (female 325 mm TL, fresh).

pelvic space. Head narrow, long, and extremely flattened, narrow ellipsoidal-lenticular in shape in cross-section at eyes. Outline of head in lateral view undulated dorsally, weakly convex on snout, weakly concave above nostrils, nearly straight above eyes, slightly concave behind eye, and convex above gills; weakly convex ventrally along lower jaws and beneath gills. In dorsoventral view, head narrowly pointed, subangular, anteriorly rounded, with gill septa expanded outwards. Snout long, extremely flattened, trowel-shaped; preoral snout length 1.18–1.42 times mouth width; tip angular and moderately pointed in dorsoventral view, with an obvious indentation just anterior to nostrils; snout very narrowly pointed in lateral view, very weakly convex above and below.

External eye opening of fleshy orbit without anterior or posterior notches, circular in shape, height 0.86–1.35 in eye length. Eyes of moderate size, length 9.69–17.23 in head length; situated laterally on head at about level of head rim; subocular ridges absent. Nictitating lower eyelids internal, with deep subocular pouches; secondary lower eyelids fused to upper eyelids.

Spiracles absent. First four gill slits subequal in height, fifth only slightly smaller, fifth about 0.82–1.09 of height of third; height of third about 7.23–10.26 in head length and 0.94–2.21 times eye length. Margins of first four gill slits straight, posterior margins irregular (weakly convex to undulated); fifth gill slit weakly concave. Gill filaments not visible from outside. Upper end of highest gill slit about level with upper edge of eye. Gill-raker papillae absent from gill arches.

Nostril with large suboval incurrent apertures, prenarial groove well developed; anterior nasal flap as short, low ridge, with distinct narrowly pointed medial tip; mesonarial flaps elongate; small suboval excurrent apertures; forward of mouth by almost an eye length; width 2.81–3.82 in internarial width, 0.76–1.26 in eye length, 1.29–1.92 in longest gill-opening.

Mouth narrowly arched and moderately large; margin of lower jaw strongly convex at symphysis; width 3.11–3.79 in head length; mouth length 1.28–1.80 in mouth width. Lips not concealing anteriormost teeth when mouth is closed. Tongue large, flat and moderately rounded, filling floor of mouth. Maxillary valve narrow, width about half of eye diameter. No large buccal papillae on floor or roof of mouth behind maxillary valve. Palate, floor of mouth and gill arches covered with buccopharyngeal denticles. Labial furrows very short, barely visible when mouth closed, uppers 0.29–0.80 times as long as lowers, lowers concealed by overlapping upper lip; anterior ends of uppers far behind eyes by distance of about almost 2 eye lengths.

Teeth few, 25–28 (n=7)/23–28 (n=8) rows or 48–56 total rows (both jaws), 2–3 series functional. Teeth not arranged in diagonal files, no toothless spaces at symphysis. Tooth formula (n=8): upper jaw 12–14 + 1 + 12–14; lower jaw 11–14 + 1–2 + 11–13. Upper teeth with slender, strongly oblique, blade-like cusps, without cusplets or serrations; slightly arched roots; lower and more oblique posteriorly; anterior teeth strongly sexually dimorphic with those of adult males greatly elongate and flexuous, clearly visible in ventral view when mouth closed. Lower teeth similar in size and shape to upper teeth.

Lateral trunk denticles of adult male (CSIRO H 6227–01, Fig. 5) very small, imbricate, tri- to multicuspid with a strong medial cusp flanked by a pair of slightly shorter lateral cusps and sometimes a second pair of much smaller lateral cusps; crowns about 1.5 times long as wide, with 3 prominent longitudinal ridges (medial ridge slightly stronger and more pronounced) that extend entire length of crown onto cusps.

Pectoral fins small, subtriangular, very weakly falcate; anterior margin slightly convex to nearly straight, apices somewhat angular; posterior margin very shallowly concave; free rear tip moderately rounded to angular, inner margin convex; base very broad, 47–60% of fin length; length from origin to rear tip 1.02–1.17 times in anterior margin length; slightly greater in area than first dorsal fin; origin situated beneath interspace of fourth and fifth gill slits; fin apex about opposite distal third of inner margin when fin is elevated and adpressed to body.

Pelvic fins small, triangular, not falcate; length of anterior

Table 1. Ranges and means of proportional dimensions as percentages of total length for *Scoliodon macrorhynchos*, *S. laticaudus*, and the holotype of *S. muelleri* (MNHN 1041).

	S. macrorhynchos n = 21			*S. laticaudus* n = 7			*S. muelleri*
	Min.	Max.	Mean	Min.	Max.	Mean	Holotype
TOT (mm)	236	562	404	169	524	323	490
PRC	73.6	77.9	76.9	75.6	77.5	76.8	78.0
PD2	61.5	66.5	64.8	62.6	65.4	64.4	65.3
PD1	33.0	38.1	35.5	35.1	38.8	36.8	35.5
HDL	21.3	25.4	23.2	23.7	29.1	25.4	21.5
PG1	16.5	20.1	18.4	18.2	23.5	20.2	17.1
POB	8.5	11.2	9.8	9.4	12.6	10.5	8.9
POB (horiz.)	7.0	10.4	8.8	8.2	11.3	9.5	8.1
POR	7.2	9.7	8.6	7.7	11.1	9.2	7.1
PRN	6.3	8.4	7.4	7.2	9.1	8.0	6.6
PRN (horiz.)	5.4	7.8	6.8	6.4	8.2	7.3	5.9
PP1	20.1	24.6	22.9	24.0	26.4	24.8	22.1
PP2	43.8	48.7	46.2	45.2	48.4	46.5	43.9
SVL	45.4	50.4	47.8	46.3	49.2	47.8	45.9
PAL	54.8	58.6	56.9	56.7	59.9	58.3	57.3
IDS	17.9	22.2	19.8	16.1	20.1	18.4	21.7
DCS	7.6	9.4	8.3	7.2	9.3	7.8	8.3
PPS	16.8	21.6	19.2	16.7	19.7	17.8	18.5
PAS	4.8	7.5	6.1	5.2	7.5	6.9	9.0
ACS	6.7	9.1	7.8	6.4	9.1	7.6	7.5
EYL	1.3	2.4	1.7	1.5	2.2	1.9	1.6
EYH	1.5	2.1	1.7	1.3	2.5	1.9	1.3
INO	7.5	10.3	8.4	7.5	11.2	9.1	7.4
NOW	1.4	2.1	1.7	1.4	2.0	1.7	1.5
INW	4.9	6.4	5.7	4.9	6.9	6.0	4.9
ANF	0.2	0.6	0.4	0.2	0.6	0.4	0.3
MOL	3.5	5.2	4.5	4.9	5.6	5.1	4.5
MOW	5.7	7.6	6.6	6.0	7.6	6.8	6.2
ULA	0.1	0.5	0.3	0.2	0.6	0.4	0.2
LLA	0.3	0.8	0.6	0.8	1.2	1.0	0.9
GS1	2.2	3.1	2.6	2.3	3.1	2.6	2.3
GS3	2.3	3.3	2.8	2.5	3.8	3.1	2.4
GS5	2.3	3.1	2.6	2.2	3.2	2.7	2.3
HDH	7.0	10.6	9.2	6.1	10.2	8.7	8.7
TRH	7.8	13.1	10.4	7.9	10.8	9.6	9.4
TAH	7.5	11.3	9.0	6.3	10.2	8.0	8.5
CPH	4.0	5.0	4.4	3.9	4.5	4.1	3.9
HDW	7.9	10.8	9.5	7.3	9.4	8.6	8.0
TRW	7.1	11.8	9.2	6.4	8.5	7.8	6.6
TAW	4.6	6.5	5.5	4.1	5.6	5.0	5.4
CPW	2.2	3.7	3.0	1.9	2.7	2.4	2.5
P1L	9.9	11.7	10.8	10.2	12.1	11.0	10.5
P1A	9.2	11.5	10.6	9.5	12.1	10.9	11.3
P1B	5.4	6.6	5.9	4.5	6.6	5.4	5.2

Table 1. cont'd.

	S. macrorhynchos			*S. laticaudus*			*S. muelleri*
	n = 21			n = 7			
	Min.	Max.	Mean	Min.	Max.	Mean	Holotype
P1H	7.5	9.9	9.0	7.8	10.3	9.1	9.8
P1I	5.0	6.2	5.7	5.2	6.2	5.7	5.5
P1P	6.8	9.5	8.2	6.3	10.6	8.4	9.0
P2L	6.9	8.3	7.7	7.3	8.7	7.9	8.2
P2A	4.3	5.6	4.9	4.7	5.4	5.0	4.7
P2B	4.4	5.9	5.3	4.7	5.6	5.2	5.2
P2H	2.7	4.2	3.5	3.2	4.3	3.8	3.9
P2I	2.4	3.4	2.8	2.2	3.7	3.1	3.5
P2P	3.9	5.1	4.3	3.4	5.3	4.3	4.5
CLO	6.6	10.0	8.1	6.0	9.0	7.5	7.3
CLI	9.1	12.1	10.5	8.4	11.8	10.1	10.1
CLB	1.1	1.4	1.2	1.2	1.4	1.3	1.0
D1L	12.9	15.5	13.8	13.3	15.6	14.0	13.3
D1A	11.2	14.0	12.6	11.1	13.5	12.3	12.6
D1B	8.8	11.0	10.0	9.2	10.9	10.0	8.9
D1H	6.5	8.4	7.4	6.6	8.3	7.6	8.6
D1I	3.5	4.8	4.1	3.8	5.1	4.2	4.8
D1P	6.2	8.9	7.5	6.7	9.2	7.9	8.5
D2L	7.2	8.5	7.9	7.5	9.3	8.5	8.3
D2A	3.7	5.0	4.4	4.3	5.5	4.8	4.1
D2B	3.5	4.8	4.1	4.0	4.8	4.4	4.0
D2H	1.4	2.0	1.7	1.7	2.2	2.0	1.9
D2I	3.5	4.4	3.9	3.2	4.7	4.1	4.2
D2P	3.7	4.7	4.1	3.8	5.3	4.4	4.9
ANL	11.1	14.1	12.7	11.4	13.0	12.1	13.5
ANA	4.9	7.8	6.4	5.1	6.7	6.3	6.1
ANB	7.9	11.2	9.8	8.0	9.3	8.9	10.3
ANH	3.0	3.8	3.3	2.8	3.7	3.3	3.0
ANI	2.8	3.5	3.2	3.0	3.9	3.3	3.3
ANP	6.7	8.9	7.7	6.6	8.1	7.3	8.4
CDM	21.9	25.6	23.1	22.2	24.9	23.3	22.0
CPV	8.0	10.5	9.0	8.5	10.2	9.2	9.5
CPL	3.2	4.8	4.1	3.4	4.7	4.0	3.9
CPU	9.1	12.3	10.5	9.5	11.5	10.3	10.4
CFW	5.9	6.8	6.3	5.6	7.5	6.4	5.4
CFL	7.8	9.8	8.6	7.8	9.7	8.9	8.0
CST	3.5	5.3	4.1	3.9	5.6	4.5	4.2
CTR	4.9	7.3	6.0	4.5	7.4	5.8	5.9
CTL	7.2	9.3	8.1	7.6	8.9	8.2	7.9
DAO	6.0	9.1	7.3	4.6	6.2	5.5	6.9
DAI	0.7	2.6	1.7	0.5	2.2	1.4	1.1
DPI	11.0	14.6	13.0	10.9	12.7	11.6	12.6
DPO	4.8	7.1	5.9	4.4	6.2	5.4	5.1
PDI	2.4	4.7	3.7	2.8	3.9	3.3	3.1
PDO	13.5	19.0	15.6	12.9	16.4	14.6	18.1

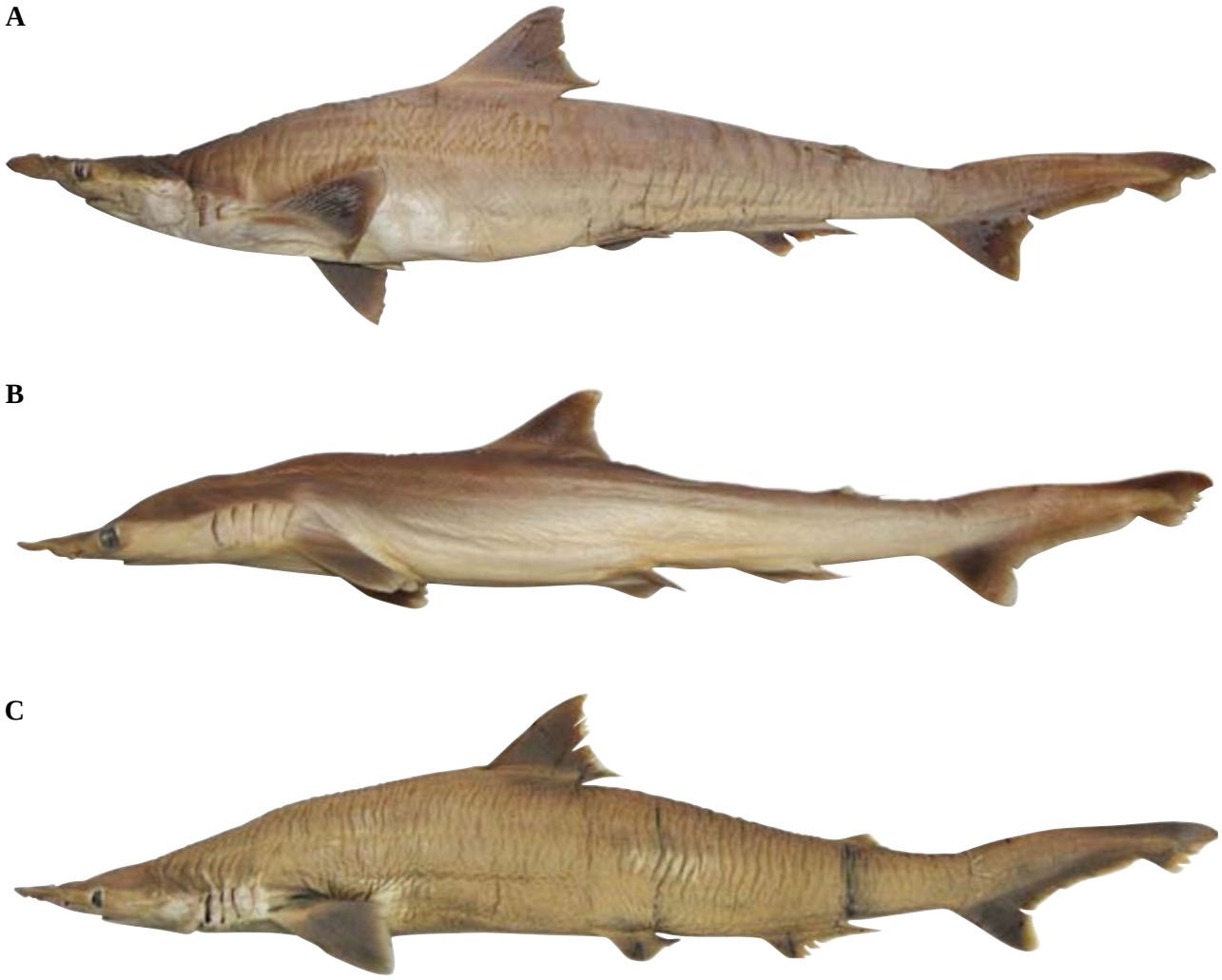

Figure 3. Lateral view of Bleeker's specimens of *Scoliodon macrorhynchos*: A. RMNH 7369 (1 of 2), female 426 mm TL; B. RMNH 7369 (2 of 2), female 236 mm TL; C. BMNH 1867.11.28.190, female 466 mm TL.

margin 0.35–0.43 of pectoral-fin anterior margin; area less than that of anal fin; anterior margin nearly straight and slightly concave near base; apices broadly rounded; posterior margin nearly straight; free rear tip bluntly rounded, inner margin nearly straight with a basal convexity. Claspers of adult males moderately long, relatively broad, slender, not tapering sharply distally, outer length 7.1–10.0% TL, base width 13.6–16.7% of outer length; extending to just anterior of anal-fin origin; clasper glans extending to about half of clasper outer length.

First dorsal fin small, broadly triangular, not falcate; anterior margin broadly convex (weakly concave basally); apex subangular; posterior margin distally straight and basally strongly concave; free rear tip acutely pointed, inner margin shallowly concave; origin posterior to pectoral-fin free rear tips, midpoint of base 1.61–2.94 times closer to pelvic origins than pectoral insertions; insertion just anterior to pelvic-fin origin, free rear tip over posterior half of pelvic-fin bases; posterior margin arcing very slightly posteroventrally from apex then abruptly posteroventrally on basal third; insertion about level with fin apex. First dorsal fin base 1.69–2.28 in interdorsal space, 2.03–2.70 in dorsal caudal margin; height 1.14–1.57 in base; inner margin 1.51–2.20 in height, 2.08–3.02 in base.

Second dorsal fin very small, low, narrowly triangular; height 0.18–0.27 times first dorsal-fin height, base 0.35–0.45 times first dorsal-fin base; anterior margin nearly straight to very weakly concave; apex broadly subangular; posterior margin very shallowly concave; free rear tip acutely pointed, inner margin very long, nearly straight; origin well behind pelvic-fin insertions and about opposite posterior third of anal-fin base; insertion just posterior to anal-fin origin; rear tip posterior to anal-fin free rear tip and anterior of dorsal caudal-fin origin by 0.85–1.40

times its inner margin; posterior margin curving strongly posteroventrally from apex; insertion about level with fin apex. Second dorsal-fin base 1.59–2.40 in dorsal–caudal space; height 1.99–3.50 in base; inner margin 2.06–2.77 in height, 0.87–1.30 in base.

Anal fin large, long, relatively low, not falcate, more than 4 times area of second dorsal fin; height 1.73–2.48 times second dorsal-fin height, base length 1.86–3.09 times second dorsal-fin base; anterior margin concave basally and distally nearly straight; apex subangular; posterior margin nearly straight for entire length; free rear tip acutely pointed, inner margin nearly straight; origin well forward of second dorsal-fin origin; insertion slightly anterior of second dorsal-fin insertion, well posterior to fin apex by about 1.5 times inner margin length; free rear tip in front of lower caudal-fin origin by about 1.5 times its inner margin length; posterior margin evenly slanting strongly posterodorsally for its entire length. Anal-fin base expanded anteriorly as long preanal ridges, about a third length of rest of base. Anal-fin base 0.61–1.02 in anal–caudal space; height 2.27–3.72 in base; inner margin 0.81–1.15 in height, 2.29–3.58 in base.

Caudal fin relatively short, narrow-lobed and asymmetrical, with short terminal lobe and prominent, moderately long, subtriangular ventral lobe; dorsal caudal margin proximally and distally convex, and slightly concave anterior to subterminal notch, with prominent lateral undulations; preventral margin weakly convex to nearly straight, tip of ventral caudal-fin lobe narrowly rounded to subangular; lower postventral margin nearly straight; upper postventral margin very slightly concave to nearly straight anteriorly, weakly convex posteriorly, moderately convex at subterminal notch; notch between postventral margins relatively shallow, forming a 130–140° angle; subterminal notch a narrow, deep slot; subterminal margin slightly concave to almost straight, terminal margin irregular and shallowly concave, lobe formed by these margins subtriangular, tip of tail narrowly rounded. Length of dorsal caudal margin 3.83–4.48 in precaudal length, preventral caudal margin 2.23–2.93 in dorsal caudal margin, terminal lobe from caudal tip to subterminal notch about 2.62–3.31 in dorsal caudal margin, subterminal margin length 1.16–1.84 in terminal margin.

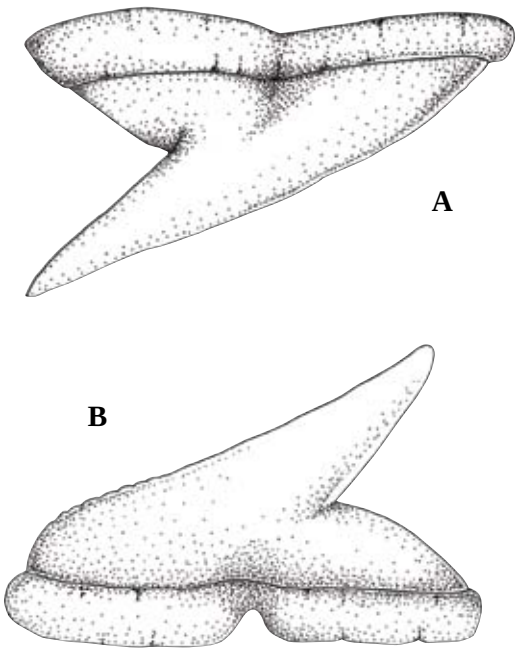

Figure 4. *Scoliodon macrorhynchos* CSIRO H 7076–02 (female 511 mm TL): A. upper anterior tooth; B. lower anterior tooth. Illustrations by Lindsay Marshall.

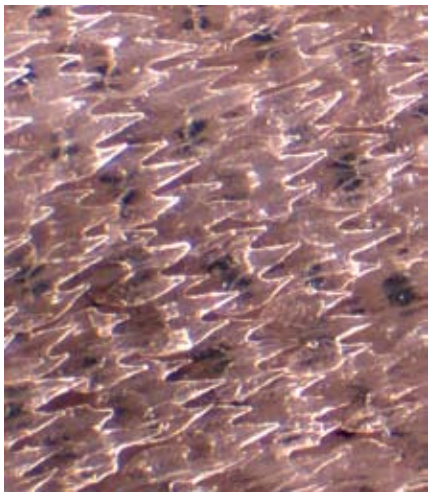

Figure 5. Flank denticles of *Scoliodon macrorhynchos* CSIRO H 6227–01 (adult male 387 mm TL). Field of view 0.7 mm.

Counts of total vertebral centra (TC) 149–171 (n=13), precaudal centra (PC) 98–114 (n=13) monospondylous precaudal (MP) centra 44–50 (n=12), diplospondylous precaudal (DP) centra 53–64 (n=12), diplospondylous caudal (DC) centra 49–59 (n=13); MP centra 29.1–30.7%, DP centra 35.5–38.3%, and DC centra 32.3–34.9% of TC centra. Ratios of DP/MP centra 1.18–1.31, DC/MP centra 1.07–1.18. Last few MP centra before MP–DP transition enlarged and forming a 'stutter zone' of alternating long and short centra, with transition often difficult to interpret.

COLORATION.— When fresh: greenish-bronze dorsally, laterally graduating to off-white ventrally; dorsal midline and head distinctly darker than subdorsal region. Demarcation of light and dark surfaces (waterline) of head sharp, extending along lateral margin of snout above eye through to upper edges of gill slits and becoming diffuse over pectoral-fin base; in dorsal view, gill slits and rim of head white, distinctly demarcated from rest of dorsal

surface; similar contrast, but more diffuse, extends along trunk and tail. Ventral and lateral margins of eye with a diffuse dusky border, broadest anteriorly and posteriorly. First dorsal fin dusky with distinctly darker anterior margin, paler greyish white submarginal base, enlarged diffuse-edged dark greyish blotch centred over posterior basal half of fin; inner margin whitish. Second dorsal fin uniformly dusky, without obvious dark area. Caudal fin mainly dusky with narrow anterior dark margin, widening greatly over terminal lobe, maximum depth exceeding eye diameter; basal half to two-thirds of posterior margin of terminal lobe with a whitish bar; postventral margin and ventral apex narrowly whitish. Pectoral fins pale, slightly darker dorsally than ventrally; enlarged brownish grey blotch over entire base (equivalent in length to pelvic fin); apex narrowly whitish. Pelvic fins and claspers uniformly white. Anal fin pale off-white to dusky. Eyes blackish, almost as dark as black pupil.

SIZE.— Specimens examined herein ranged in length from 147–562 mm TL; two specimens were subadult males with lengths of 317 and 337 mm TL, while 6 specimens were adult males of 387–562 mm TL. A study by Lam (2009) on the biology of *S. macrorhynchos* (as *S. laticaudus*) from Hong Kong waters recorded maximum sizes of 707 and 636 mm TL for females and males, respectively. Lam (2009) reported litter sizes of 3–23 (mean 10.5) pups with parturition occurring annually in June and July. She also recorded size at maturity for females and males of 397 and 377 mm TL.

DISTRIBUTION.— Occurs in the Western Central Pacific; recorded from western Indonesia, Malaysia, Gulf of Thailand, Singapore, Borneo, Philippines, China, Hong Kong, Taiwan and Japan. Not recorded from eastern Indonesia, New Guinea, northern Australia or remainder of the Oceania region. Typically found in shallow, inshore waters, most abundant near large freshwater outflows, e.g. Pearl River estuary (Hong Kong) and the large Borneo drainage systems.

DISCUSSION

Eschmeyer (2010) state that the holotype of *S. macrorhynchos* is one of two of Bleeker's specimens deposited at the Rikjsmuseum van Natuurlkjke Histoire (RMNH) in Leiden (RMNH 7369); a third Bleeker specimen is held at the British Natural History Museum (BMNH) in London. Both specimens in Leiden are females, 426 mm TL and 236 mm TL (RMNH 7369), and the specimen in London is also a female of 466 mm TL (BMNH 1867.11.28.190). However, the original description by Bleeker (1852) refers to a 218 mm TL male (as "masculini"). Thus, none of the 3 female specimens above represent the holotype of *S. macrorhynchos*.

Hubrecht (1973) provides lists of all of Bleeker's specimens auctioned in 1879 and these lists clearly state that 4 specimens of *S. macrorhynchos* were auctioned, two in the Group A and one in each of the Group B and Group C collection lists. The Group A collection, which was acquired by Hubrecht for the Leiden museum, is considered the most important collection as it included Bleeker's type specimens (Whitehead *et al*., 1966; Boeseman, 1973). The Group B collection was acquired by W. Berlin at Amsterdam, and Group C by E. Gerrard at the British Museum in London (Boeseman, 1973). Thus, it is possible that the holotype of *S. macrorhynchos* was not included in the Group A collection, but instead in the Group B collection, currently housed in the Zoological Museum Amsterdam (ZMA). Bleeker was also known to occasionally discard or donate his holotypes when a better specimen was obtained (R. Fricke, pers. comm.), which may have been the case for this species.

The three genetic analyses conducted on the *Scoliodon* samples obtained (Figs 6a–c) show consistent and compatible topologies. Three distinct clades are evident corresponding to three species of *Scoliodon*. It is noteworthy that the sample of individuals shows little within-species variation, and the little that there is in *S. macrorhynchos* does not appear to be geographically structured. Both the Neighbour-joining (Fig. 6a) and Maximum Likelihood (Fig. 6c) analyses suggest that *Scoliodon laticaudus* is the sister species to *Scoliodon macrorhynchos*, while the specimens from the Bay of Bengal fall as the basal sister to the aforementioned two. While this may be the case, we feel that the very short branch length separating the two specimens from the Bay of Bengal, without other supporting evidence, not sufficiently compelling to justify such a conclusion.

The genetic results presented in this paper for this genus (Fig. 6) show a third species level split from two specimens collected in the Bay of Bengal off Thailand (probably from Myanmar waters). These two specimens are more divergent than the *S. macrorhynchos* and *S. laticaudus* clades. *Scoliodon laticaudus* (Fig. 7a) is one of the most abundant sharks off the west coast of India, but appears to be much less common off the east coast (Raje *et al*., 2007). Indeed, most studies on the biology of this species from India are from the west coast of India. Members of this genus are shallow water species which appear to prefer coastal areas adjacent to major river outflows. It is thus possible that the smaller number of large river systems and the much narrower shelf area on the east coast of India is, or at least was, a substantial barrier to such species. East of this area is the northern end of the Bay of Bengal where major river systems are once again present and a much wider shelf. Alternatively, when Sri Lanka was part of the Indian mainland, the southern part of Sri Lanka with its narrow shelf and deeper waters may have been a substantial barrier to a coastal species. If such a barrier-effect has occurred, then the *Scoliodon* present in the Bay of Bengal area, including northeastern India, are possibly conspecific with the two Thailand specimens mentioned above.

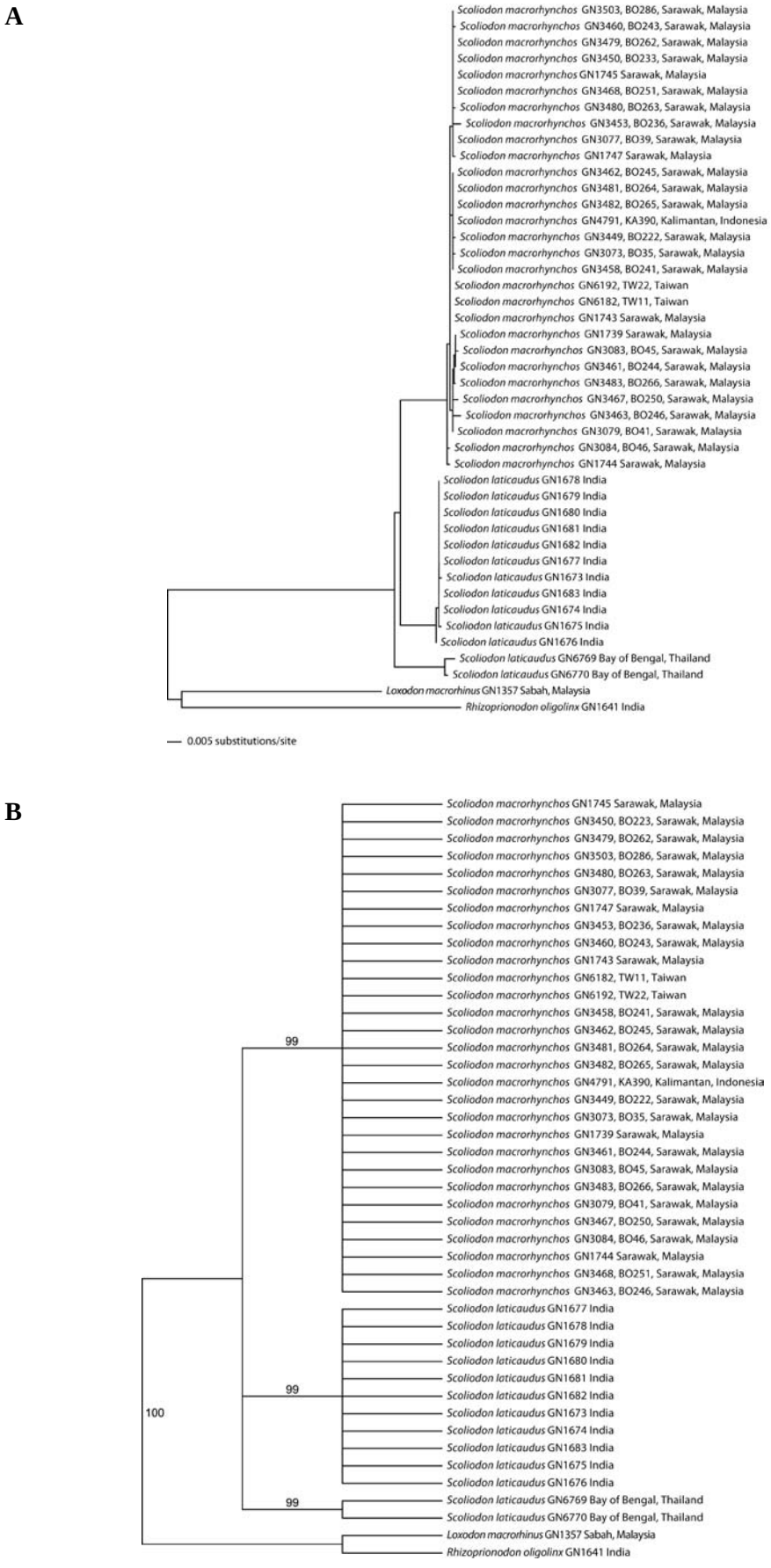

Figure 6. Neighbour-Joining trees using a GTR+I+Γ model (General Time Reversible + Invariant sites + gamma distributed rates) for the genus *Scoliodon* based on: A. K2P distance; B. Parsimony Bootstrap with 1000 replicates; and C. Maximum Likelihood. Model parameter values were optimized recursively for the Likelihood analysis as the search progressed.

Figure 6. cont'd.

Müller & Henle (1839) described *Carcharias* (*Physodon*) *muelleri* from 'Bengale' which was subsequently synonomised with *S. laticaudus* by Compagno (1984) (Fig. 7b). The location of the holotype of 'Bengale' refers to the historical geographical area of Bengal in the northeast Indian subcontinent located at the northern end of the Bay of Bengal. Thus, it is a distinct possibility that *S. muelleri* is a valid taxon which is restricted to the Bay of Bengal. Further investigation is required to determine whether this is the case and obtaining viable DNA from the holotype of *S. muelleri* would assist in this investigation. Determining an accurate geographical range for each of the three species is crucial for future management plans for this species, especially as *Scoliodon* forms such a large proportion of the shark catches in coastal waters of India.

The morphometric data show that some features show substantial intraspecific variation of up to 5.2% in *S. macrorhynchos*. The characters showing the most variation (i.e. >4% TL) were those associated with head and snout measurements (e.g. head length, prepectoral length), pre-fin and pre-vent lengths and inter-distances between fins. Comparison of large females (n=9) with adult males (n=6) did not show any substantial differences between the sexes, with the exception of PDO (pelvic midpoint to second dorsal-fin origin) which was usually greater in adult males than large females, i.e. 15.9–19.0 vs. 13.6–16.2% TL. The large number of specimens measured has enabled some of this variation to be attributed to ontogenetic changes. Comparison of small specimens (236–353 mm TL, n=8) with large specimens (426–562 mm TL, n=10) revealed a number of substantial differences associated with head measurements. Smaller specimens have a longer and narrower head than larger specimens which is illustrated by the following morphometric differences: head length 23.4–25.4 vs. 21.3–23.0% TL, preorbital length 9.7–11.2 vs. 8.5–9.7% TL, preoral length 8.9–9.7 vs. 7.2–8.5% TL, prepectoral length 23.5–24.6 vs. 20.1–22.7% TL, interorbital space 8.2–10.3 vs. 7.5–8.4% TL, and internarial width 5.7–6.4 vs. 4.9–5.8% TL.

Scoliodon macrorhynchos is very similar in morphology to *S. laticaudus* with only a small number of mean differences (ranges partly overlapping) apparent when comparing all specimens together, i.e. mean head length 23.2 vs. 25.4% TL, mean prepectoral length 22.9 vs. 24.8% TL and mean lower labial furrow length 0.6 vs. 1.0% TL. The main detectable morphological difference was the second dorsal-fin to anal-fin origin measurement which was greater in *S. macrorhynchos* (6.0–9.1% TL,

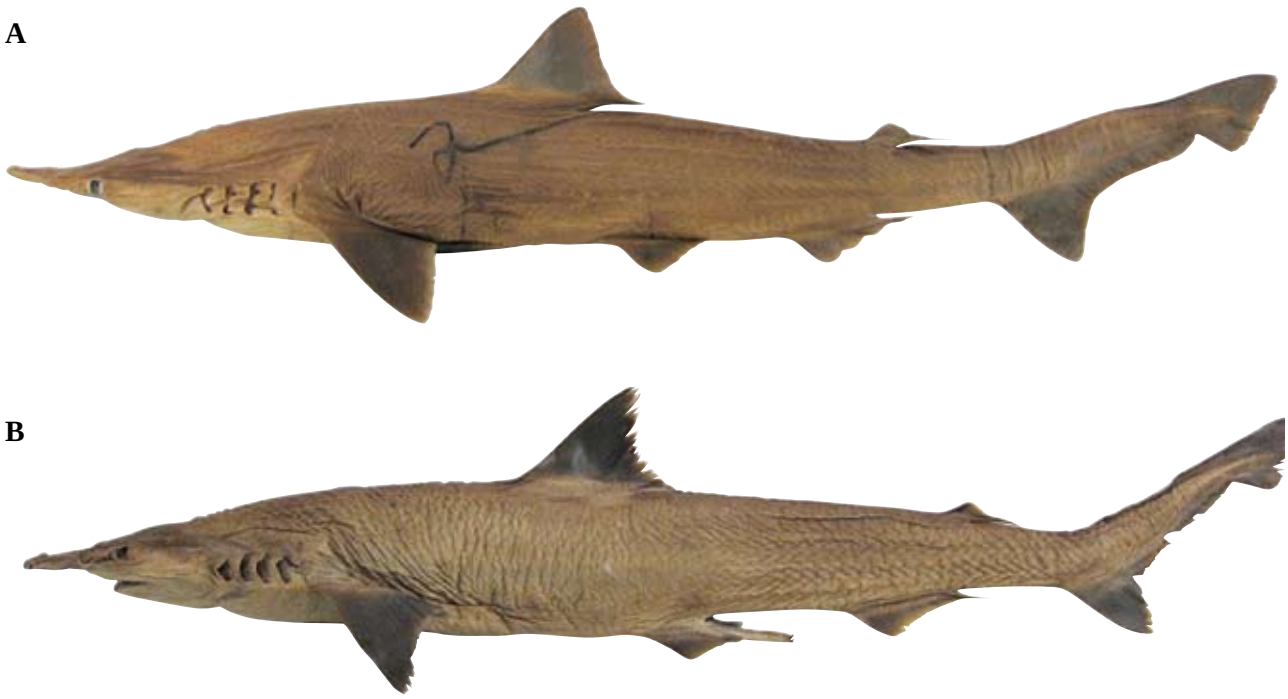

Figure 7. Lateral view of: A. *Scoliodon laticaudus* (MNHN 1123, female 524 mm TL); B. *Scoliodon muelleri* holotype (MNHN 1041, adult male 490 mm TL).

mean 7.3% TL) than in *S. laticaudus* (4.6–6.2% TL, mean 5.5% TL). Given the ontogenetic differences noted above for *S. macrorhynchos*, it is more useful to compare similar size specimens of the two species. The large specimens of *S. macrorhynchos* (426–562 mm TL, n=10) differed from the two large *S. laticaudus* specimens (425 and 524 mm TL) in having a shorter head (length 21.3–23.0 vs. 23.7–24.0% TL), shorter prepectoral length (20.1–22.7 vs. 24.1% TL), slightly shorter claspers in adult males (10.4–11.2 vs. 11.8% TL), and a slightly longer anal fin (its length 12.4–14.1 vs. 11.4–12.1% TL). There were few differences between the smaller specimens of the two species which is not surprising given the larger intraspecific variation of smaller specimens in each of the species compared to in larger specimens.

The vertebral counts for *S. macrorhynchos* appear to vary according to geographical occurrence with higher counts recorded from the higher latitude specimens from Hong Kong (TC=161–171, PC=107–114, n=6) and lower counts from the lower latitude specimens from Indonesia and Malaysia (TC=149–160, PC=98–107, n=7). These trends are also apparent in the precaudal counts provided in Springer (1964) for specimens from Japan and China (99–112, mean 106.3, n=21) versus those from Penang, Moluccas, Singapore and Batavia (97–103, mean 100.1, n=13). The numbers of precaudal centra in *S. laticaudus* from India presented by Springer (1964), 97–110, overlap completely with those recorded for *S. macrorhynchos*.

The dentition of species of *Scoliodon* show strong sexual dimorphism with the anterior teeth possessing greatly elongate and flexuous cusps (Fig. 8) that are clearly visible in ventral view with the mouth closed. Springer (1964) also recorded this condition for *S. laticaudus*, as well as in species of *Rhizoprionodon* and *Loxodon macrorhinus*. The extent of sexual dimorphism is likely to be the main reason prompting Müller & Henle (1838) to propose the subgenus *Physodon* for *Carcharias muelleri*, with a paragraph of the description detailing the long, hook-like, anteriormost teeth on the adult male holotype. In contrast, their description of *Carcharias* (*Scoliodon*) *laticaudus* is based on a female specimen that would have had much lower, oblique cusped teeth. Sexual dimorphism is generally poorly described in carcharhinid sharks, but has been reported for the centrophorid genera *Deania* and *Centrophorus* (Garrick, 1960; White *et al*., 2008), and is likely to be prevalent in many sharks.

Comparative material.

Scoliodon laticaudus: 7 specimens: MNHN 1066 (3 specimens), juvenile males 169, 187 and 258 mm TL, MNHN 1122, adult male 425 mm TL, Malabar coast, India, ~11° N, ~76° E; MNHN 1123, female 524 mm TL, Maharashtra, Mumbai, India, 18°56′ N, 72°51′ E; MNHN 1125, female 342 mm TL, Indian Ocean, exact locality not recorded; RMNH 8574, subadult male 353 mm TL, Malabar coast, India.

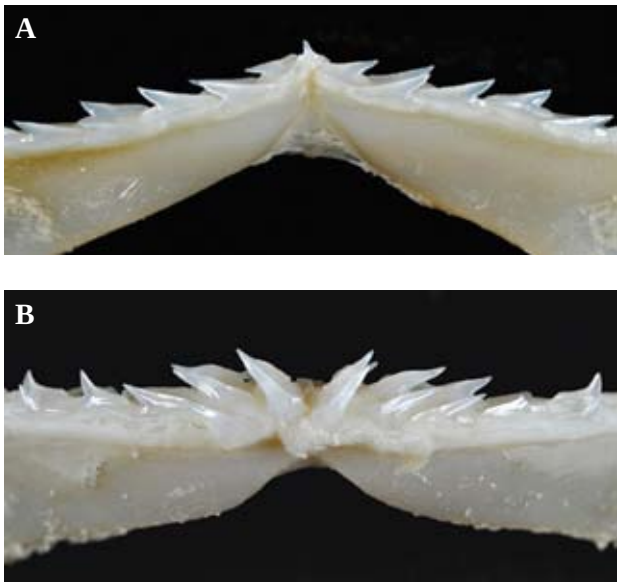

Figure 8. Central region of the lower jaw of *Scoliodon macrorhynchos*: A. adult female (CSIRO H 7076–02, 511 mm TL); B. adult male (CSIRO H 7076–04, 555 mm TL).

S. muelleri: 1 specimen: MNHN 1041 (holotype), adult male 490 mm TL, 'Bengale'.

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A new species of wedgefish, *Rhynchobatus springeri* (Rhynchobatoidei, Rhynchobatidae), from the Western Pacific

Leonard J.V. Compagno[1] & Peter R. Last[2]

[1] Shark Research Center, Iziko – Museums of Cape Town, Cape Town 8000, SOUTH AFRICA
[2] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA

ABSTRACT.— A new species of wedgefish, *Rhynchobatus springeri* sp. nov. is described from specimens collected from the Indo–Malay region, with a confirmed range extending from the Gulf of Thailand south to Java, and possibly westward to at least Sri Lanka. It is a medium-sized species to about 215 cm TL, with males reaching adulthood at about 110 cm TL. *Rhynchobatus springeri* closely resembles *R. palpebratus* in body shape and having a dark, eye-brow like marking on its orbital membrane, but differs from this species in having a lower vertebral count (113–126 vs. 130–139 total free centra), a broader preorbital snout, and more rows of white spots on the tail of adults. Other *Rhynchobatus* species in the region attain a much larger adult size, and have a relatively narrower snout and much higher vertebral counts. A revision of the group is needed to find more useful field characters.

Key words: Rhynchobatidae – *Rhynchobatus springeri* – Broadnose Wedgefish – new species – Western Pacific

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

The genus *Rhynchobatus* Müller & Henle, 1837 comprises several species of moderate-sized to giant (attaining between 0.8 and more than 3 m total length) shark-like batoids. They belong in the monotypic family Rhynchobatidae, according to the classification of McEachran *et al*. (1996), removing them from family Rhinidae and a single species *Rhina ancylostoma* Bloch & Schneider, 1801. Following FAO usage (Stehmann, 1981; Compagno & Last, 1999), *Rhynchobatus* species are termed 'wedgefishes' because of their distinctive wedge-shaped discs; other names include giant guitarfishes, white-spotted guitarfishes, and, significantly, sharkfin guitarfishes. Wedgefishes are widespread and common in inshore tropical waters of the Eastern Atlantic, Indian Ocean, and Western Pacific.

Members of the genus *Rhynchobatus* include some of the largest species of rays, with *Rhynchobatus djiddensis* attaining a total length of 3 m and *R. luebberti* reaching a weight of at least 227 kg. Two other *Rhynchobatus* species grow to at least 2–3 m length. Müller & Henle (1837, 1841) recognized only a single species in the genus *Rhynchobatus*, *R. laevis* (Bloch & Schneider, 1801). Eleven species and a subspecies have been referred to *Rhynchobatus* by various authors, but only two, the West African *R. luebberti* Ehrenbaum, 1914 and the Indo–West Pacific *R. djiddensis* (Forsskål, 1775), are generally recognised as valid and most of the remaining taxa have been synonymised with *R. djiddensis* (Garman, 1913; Fowler, 1941). Compagno & Last (1999) gave a brief review of the Western Central Pacific species as members of the family Rhinidae, including a key to species in the area and brief accounts and illustrations of *R. australiae* (Whitley, 1939), *R.* cf. *laevis* (Bloch & Schneider, 1801), and two undescribed species, referred to as *R.* sp. 1 and *R.* sp. 2. More recently, Compagno & Last (2008) described a new species, *Rhynchobatus palpebratus*, from the Indo–Malay Archipelago, and provisionally recognised 6 other taxa as valid: *Rhynchobatus australiae* Whitley, 1939 from Australia, Thailand, Philippines, Singapore, Taiwan, and Indonesia; *Rhynchobatus djiddensis* (Forsskål, 1775) from the western Indian Ocean, including southern Africa, Mozambique and the Red Sea; *Rhynchobatus laevis* (Bloch & Schneider, 1801) from Zanzibar, the Arabian Sea, Oman, the Persian Gulf, India, Sri Lanka, and Bangladesh; *Rhynchobatus luebberti* Ehrenbaum, 1914 from tropical West Africa, including Mauritania to Congo and Angola; *Rhynchobatus* sp. 1 (Compagno & Last, 1999), only known from Singapore and Java; and *Rhynchobatus* sp. 2 (Compagno & Last, 1999) found in

the Western Pacific, including the Philippines, Thailand, Sarawak, Singapore, and Java.

Wedgefishes are commonly caught as bycatch of demersal inshore fisheries wherever they occur and are important commercially for their excellent flesh and very valuable fins, which are currently important in the oriental shark-fin trade. The intense fisheries pressure on wedgefishes, and minimal biological data on any of the species, makes for concern about their conservation status; currently no species in the family is protected and fisheries are largely unregulated. In southern Africa and tropical Australia, wedgefishes are sought as game fishes by sports anglers because of their great size and strength, and powerful response when hooked.

The following paper describes one of the undescribed wedgefishes *Rhynchobatus* sp. 2, a broad snouted form with a low vertebral count.

METHODS

Proportional dimensions, expressed as percentages of total length, are given in Table 1. External measurements of *Rhynchobatus* specimens are based on batoid measurements proposed by Bigelow & Schroeder (1953), Hubbs & Ishiyama (1968), Compagno & Roberts (1982), Compagno & Randall (1987) and Randall & Compagno (1995), and the shark measurements of Compagno (1984, 2001). Terminology for enlarged dermal denticles or thorns is based on Hubbs & Ishiyama (1968). Vertebral centra, pectoral-fin radials, and crania were examined and meristic details counted from radiographs including all paratypes and 8 non-types (see also Compagno & Last, 2008). The vertebral column of *Rhynchobatus* is more differentiated than in sharks and is clarified herein: a group of vertebrae behind the cranium are fused to form a large cervical synarcual element (Garman, 1913; Compagno, 1973, 1988, 1999, 2003) containing from 25–34 segments; the synarcual element has an anterior centrum-free region of 13–21 segments and a posterior region with 11–16 embedded centra. The number of synarcual segments is determined by counting the synarcual centra and the corresponding spinal nerve foramina and canals in the anterior centrum-free region on properly exposed, high-resolution radiographs; it is often not possible to count the centrum-free region in some specimens, particularly newborn and poorly calcified individuals, although synarcual centra are usually visible. Posterior to the synarcual, the vertebral column can be subdivided into monospondylous precaudal (MP) centra in the trunk, diplospondylous precaudal (DP) centra in the precaudal tail, and diplospondylous caudal (DC) centra in the caudal fin. The MP centra have very long ribs that are reduced posteriorly before the transition to DP centra, in which the centra suddenly become smaller and two per myomere. The DC centra have strongly expanded neural and haemal arches modified as pterygiophores for the caudal fin but, for purposes of consistency, counts are delimited anteriorly at the upper caudal-fin origin as in sharks (Springer & Garrick, 1964). Counts presented here include the numbers of centra in the synarcual element, and the MP centra, DP centra, DC centra, total free centra, and total centra; centrum-free segments and total segments were not included as some of these counts proved difficult to obtain.

In *Rhynchobatus*, as in most modern elasmobranchs or neoselachians (Compagno, 1973, 1977, 1988, 1999, 2003), there are three basal cartilages to the pectoral-fin skeleton: the anterior propterygium, intermediate mesopterygium, and posterior metapterygium, which bears most of the pectoral-fin radials. *Rhynchobatus* (and various other batoids) have a space between the mesopterygium and metapterygium where `neopterygial' radials articulate directly with the synarcual. The propterygium of *Rhynchobatus* is a single, unsegmented cartilage with its front end terminating behind the nasal capsules; anterior to the propterygium are 1–8 free propterygial radials suggesting that a segmented propterygial axis, such as that present in other batoids, may have been lost in *Rhynchobatus*. The propterygium itself has 16–26 radials, the mesopterygium about 5–7 radials, the neopterygial space on the scapulocoracoid about 4–6 radials, and the metapterygium 21–29 radials. Counts presented include free, propterygial, mesopterygial, neopterygial, metapterygial, total basal radials (excluding free radials), and total radials. Cranial morphology of the new *Rhynchobatus* species is not considered in detail here but we note that *Rhynchobatus* species differ in the shape of their rostral appendices, and by the position of the anterior ends of the antorbital cartilages relative to the anterior ends of the nasal capsules.

Morphometric data in the description includes information on 6 specimen lots that were not included in the type series as their whereabouts is presently unknown, while another two lots (SU 69893 and SU 69894) still require resolution as they contain multiple specimens. Also, USNM 72480 (apparently cited by LJVC in his data files as USNM 75877 but matching USNM 72480 in size, sex and locality data) is confirmed to be a specimen of the new species (by PL), based on photos facilitated by Jerry Finan, Jeffrey Williams and Sandra Raredon at the USNM.

Material discussed in this manuscript is deposited widely in ichthyological collections following Leviton *et al*. (1985): Australian National Fish Collection (CSIRO), California Academy of Sciences (CAS), Hokkaido University Museum (HUMZ), Marine Reference Collection at Institut Penyelidikan Perikanan Sarawak (IPPS), Natural History Museum of Los Angeles County (LACM), Rijks Museum voor Natuurlijke History (now = National Museum of Natural History, Naturalis (RMNH), National Museum of Natural History (USNM), and Zoological Museum Hamburg (ZMH). Also includes two

subcollections: GVF (= George Vanderbilt Foundation collection, which was incorporated into the CAS in 1967) and SU (= Stanford University collection, which was incorporated into the CAS in 1969).

Rhynchobatus springeri sp. nov.

Figs 1–3, Table 1

Rhynchobatus sp. 2: Compagno & Last, 1999, 1422, fig.

Holotype. RMNH PISC 35839, female 410 mm TL, Jakarta (as Batavia), Indonesia, 1924.
Paratypes. 22 specimens: CAS 229747, immature male 501 mm TL, Gulf of Thailand, Thailand, 12°19′ N, 100°27′ E, 33 m, Aug. 1960; CAS 229748, immature male 600 mm TL, Gulf of Thailand, Thailand, 05 Apr. 1960; CAS 229749, female 780 mm TL, Gulf of Thailand, Thailand, 26 Jun. 1960; CAS 229750, female 561 mm TL, Gulf of Thailand, Thailand, 11°51′ N, 100°30′ E, 36 m, Aug. 1960; CAS 229751, immature male 490 mm TL, Gulf of Thailand, Thailand, 12°13′N, 100°07′E, 26 m, Jul. 1960; CAS 229752, immature male 482 mm TL, Gulf of Thailand, Thailand, 33 m, 01 Jul. 1960; CAS 229754, immature male 497 mm TL, Gulf of Thailand, Thailand, 12°15′ N, 100°17′ E, 36 m, Mar./Apr. 1961; CAS 229755, female 379 mm TL, Gulf of Thailand, Thailand, 12°23′ N, 100°33′ E, 36 m, Dec. 1960; CAS 229757, immature male 443 mm TL, Gulf of Thailand, Thailand, 12°19′ N, 100°27′ E, 33 m, Aug. 1960; CAS 229758, female 486 mm TL, Gulf of Thailand, Thailand, 12°11′ N, 100°41′ E, 37 m, Jan. 1961; CAS 229759, immature male 469 mm TL, Gulf of Thailand, Thailand, 12°13′N, 100°07′ E, 26 m, Jul. 1960; CAS 229760, female 900 mm TL, Gulf of Thailand, Thailand, 05 Apr. 1960; CSIRO H 7113–01, female 413 mm TL, Gulf of Thailand, Thailand, 16 m, 27 Jun. 1960; CSIRO H 7113–01, immature male 388 mm TL, Gulf of Thailand, Thailand, 12°06′ N, 101°11′ E, 37 m, Dec. 1960/Jan. 1961; HUMZ 96569, immature male 466 mm TL, off Kuching, Sarawak, Malaysia, 03°39′ N, 110°42′ E, 12 Dec. 1971; HUMZ 96570, adolescent male, South China Sea, Nov./Dec. 1971; HUMZ 117525, adolescent male 711 mm TL, off Kuching, Sarawak, Malaysia, Dec 1966; IPPS 2009–338, adult male 1126 mm TL, near Kuching Marine Labs (Sarawak), Malaysia, 06 Nov. 2009; RMNH PISC 35840, immature male 390 mm TL, Java Sea, Indonesia, Jan. 1911; SU 13330, female 480 mm TL, Manila, Philippines; ZMH 10259, immature male 447 mm TL, Java, Indonesia, 1855; ZMH 101280, female 567 mm TL, Gulf of Thailand, Thailand, 20–40 m, Aug./Sep. 1961.
Other material. 9 specimens: CAS - GVF 2125 unreg, female 2130 mm TL, Gulf of Thailand, Thailand, 05 Apr. 1960; CAS - GVF 2239 unreg, immature male 743 mm TL, Gulf of Thailand, Thailand, 26 Jun. 1960; CAS - GVF 2361 unreg, adult male 1250 mm TL, Gulf of Thailand, Thailand, 12°20′ N, 100°36′ E, 25 m, Aug. 1960; CAS – GVF unreg, immature male 450 mm TL, Philippines; LACM unreg, female 498 mm TL, LACM unreg, immature male 430 mm TL, Singapore; SU 69893, female 450 mm TL, Manila, Philippines, 31 May 1931; SU 69894, immature male 395 mm TL, Singapore, Mar. 1934; USNM 72480, female 610 mm TL, Java, Indonesia.

DIAGNOSIS.— A moderate-sized species of the genus *Rhynchobatus* with the following combination of characters: a broadly wedge-shaped snout; preoral snout 16–22% of total length; eye small, length 3.1–4.0 in preorbital snout; interorbital space 2.2–2.7 in preorbital snout; mouth hardly bowed, with a strong indentation on upper jaw near symphysis and strong protuberance on lower jaw; tooth rows in upper jaw about 52 (based on holotype); no spines on dorsal snout; no rostral spines or spines at dorsal tip of snout; supraorbital spines small but well differentiated, extending from preorbit to end of spiracle; spines of mid-dorsal row relatively well developed; two obvious rows of small scapular spines on each side; origin of first dorsal fin over origin of pelvic-fin bases; predorsal space 42–48% of total length; colour pale greyish green above with 3–4 rows of large, white spots extending along the tail; black pectoral marking prominent, usually closely surrounded with 4 white spots (occasionally 3); anterior pectoral disc with a narrow whitish margin; orbital membrane with a pair of dark, widely spaced, recurved lines; no alternating light and dark markings on interorbital space; propterygial radials 1–8 + 20–23, mesopterygial radials 4–6, neopterygial radials 4–7, metapterygial radials 23–29, total radials 57–68 (inc. free radials); vertebrae with 12–14 synarcual centra, 18–28 monospondylous precaudal centra, 78–88 precaudal free centra, 33–40 diplospondylous caudal (free) centra, 113–126 total free centra, 127–139 total centra (including synarcual centra).

DESCRIPTION.— Body relatively robust; snout in front of eyes bluntly angular to obtusely wedge-shaped, angle of about 50° in holotype. Lateral margin of anterior half of snout almost straight, then becoming distinctly convex between eye and origin of pectoral fin. Preorbital length about 3.2 in holotype (2.9–3.4 in paratypes) times interorbital width. Preoral length 3.5 (3.0–3.4) times mouth width. Disc width across pectoral-fin apices 73% (69–84%) of disc length from snout tip to pectoral-fin free rear tips. Head strongly depressed, trowel-shaped, disc thickness 1.2 (1.4 in one paratype) times in interorbital space; ventral head length 3.2 (3.1–3.7) times in total length; surface between eyes and spiracles almost flat. Precloacal length 87% (74–92%) of length of tail from anterior vent to caudal-fin tip. Tail depressed (somewhat dehydrated in holotype); in cross section, rounded dorsally, less so ventrally, angular laterally, tapering evenly from pelvic-fin insertions. Width of tail at first dorsal-fin insertions of holotype 1.3 times interspiracular distance. Lateral keels of tail extended forward as a thick angular edge along precaudal tail, almost reaching first dorsal insertion; strongly differentiated on caudal fin.

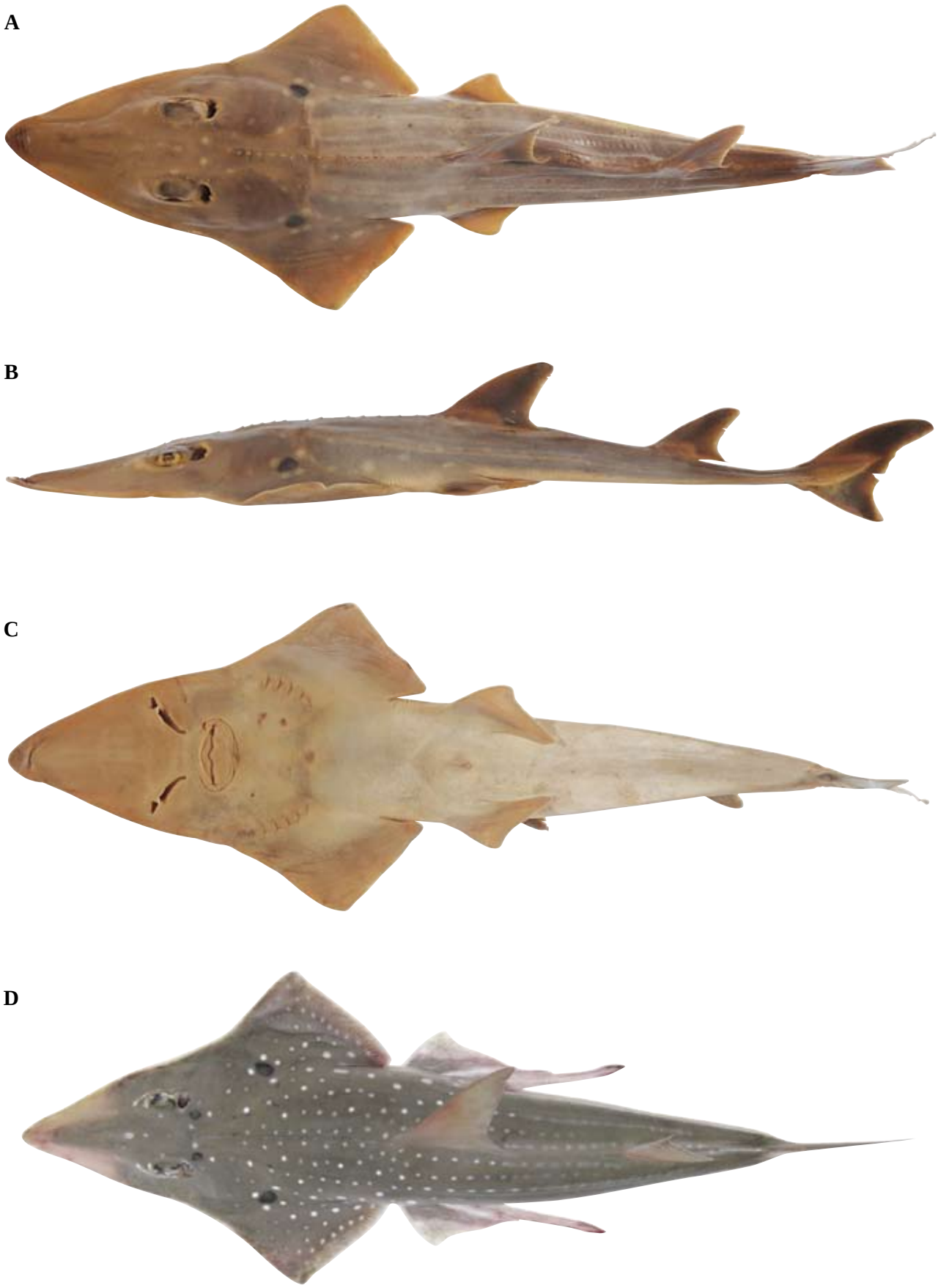

Figure 1. *Rhynchobatus springeri* sp. nov.: A. dorsal view of female holotype (RMNH PISC 35839, 410 mm TL, preserved); B. lateral view of holotype; C. ventral view of holotype; and D. reconstructed dorsal view of adult male paratype (IPPS 2009–338, 1126 mm TL, fresh), specimen missing dorsal fins and part of right pelvic fin.

Horizontal eye (eyeball) diameter about 76% (64–79%) of interspiracular width, distance from anterior margin of orbit to posterior margin of spiracle subequal to interspiracular width; greatest dimension of spiracles 46% (39–57%) of horizontal eye diameter; distance between spiracle and eye about half horizontal eye diameter, membrane of orbit almost continuous with spiracular opening. Spiracle dorsolateral, anterior margin with a strong valve, posterior margin with two anteriorly directed spiracular folds; outer fold slightly taller and larger than the inner fold.

Nostrils diagonal, forming about a 45° angle with body axis, anterior ends more lateral. Nasal cavity fully exposed, without dividing flaps; aperture straight anterolaterally, recurved posteromedially. Anterior nasal flap narrow, low, anteromedial on nasal aperture, inserted near midlength of nasal aperture; anterior process short, bilobed, its base length about twice as long as its width. Posterolateral nasal flap low, narrow and elongated, weakly lobate; originating just behind anterior lateral edge of incurrent aperture, extending posteriorly to about midlength of nasal aperture. Posterior nasal flap low, short based; joined to undersurface of posterolateral flap at about anterior third of its length, junction concealed beneath posterolateral nasal flap; inserted near midlength of nostril. Nostril width 1.2 (1.1–1.5) times in internarial width. Mouth opening somewhat arcuate, weakly undulating to nearly straight laterally; strong medial depression on upper jaw corresponding to a very prominent anterior extension at symphysis of lower jaw; much weaker corresponding depressions and convexities laterally. Labial folds and furrows short, but well developed at corners of mouth. Shallow pockets, circumoral grooves, and low folds and depressions, surround jaws laterally to labial folds; depressions most prominent on lower jaw. Teeth in differentiated serial rows, about 52 in upper jaw of holotype. First four gill openings subequal in length, the fifth slightly shorter. Third gill opening 3.2 (1.9–2.9) in internarial width, 3.8 (2.6–3.6) times in nostril length, 1.2 (1.1–1.8) times length of fifth gill opening.

Dermal denticles covering all of body surface (based on holotype and paratype RMNH PISC 35840), varying in shape across different parts of body; on dorsal surface, minute, dense but not imbricate, no obvious skin exposed between them; those on orbital membrane slightly smaller than those on interorbit; an indistinct patch of enlarged denticles present in front of eyes, length of patch about half length of eye. Dorsal denticles with slender pedicels and flat elevated crowns; crowns on trunk flattened, broad, subcircular, irregularly rounded anteriorly, unicuspidate or weakly tricuspidate posteriorly, usually with low medial and lateral ridges. Ventral denticles usually lacking cusps, strongly imbricate; subequal in size to those of dorsal surface.

Small, variable-sized thorns present on dorsal surface of body and tail; present on orbital margin, along dorsal midline, and in scapular region, those between nuchal and mid-scapular regions largest; rostral thorns absent. Thorns on midline of disc and tail long based, narrow, strongly oblique, bases partially embedded in skin; their surface mostly smooth, with corrugated anterior margins; largest thorns keel-like, posterior outer edges forming a sharp point, bases surrounded by a narrow naked perimeter. Orbit with continuous series of variably sized thorns; series extending along inner margin of orbit from anterior mid-eye to posterior margin of spiracle; mostly in a single row, approximately 12 on each side in holotype; row partly interrupted above anterior spiracle (partially subdivided into orbital and spiracular groups of thorns). Mid-dorsal series of thorns present before first dorsal fin (predorsal series) and between dorsal fins (interdorsal series); absent behind second dorsal fin. Predorsal thorns on a low dermal ridge in a single row, extending from anterior nuchal region to end of free rear tip of pectoral fin; more or less evenly spaced; about 14 thorns of varying size in holotype. Interdorsal thorns poorly defined, partly naked dermal ridge, extending in a single feeble row from free rear tip of first dorsal fin to about half eye diameter anterior to second dorsal-fin origin; much smaller than predorsal thorns, 4 in holotype (paratype RMNH PISC 35840 with about 14 thorns). A row of two short, disjunct patches (rows) of scapular thorns on each side of disc in holotype; positioned just forward of level of apices of pectoral fins; anterior patch with 3–4 thorns, its length about half of eye diameter; posterior patch with 2–3 thorns, short, less than half eye diameter; lateral patches absent in holotype.

Dorsal fins similar in shape, raked, shark-like, with strongly convex anterior margins (shallowly concave at base), bluntly pointed apices, deeply concave posterior margins, sharply acute free rear tips, and straight inner margins. Inner margin of first dorsal fin 67% (65–119%) of its base length. First dorsal fin considerably larger than second; origin about over origins of pelvic fins; free rear tip opposite or slightly behind free rear tips of pelvic fin. Interdorsal space 2.1 (1.9–2.9) times length of first dorsal base, about 3.0 (2.9–4.4) of length of second dorsal-fin base. Caudal fin rather short; dorsal caudal margin 6.3 (5.8–6.8) in total length, subequal to interdorsal space. Dorsal caudal margin moderately convex, slightly concave near its origin; tip bluntly pointed. Preventral caudal margin weakly convex, less so anteriorly; ventral lobe well developed, strong, angular (relatively shorter and less well-defined in juveniles). Lower postventral caudal margin short, weakly concave, 3.1 (3.0 in one paratype) in length of upper. Upper postventral margin weakly concave. Caudal axis elevated slightly, forming a narrow angle to body axis. Pectoral fins originating at about spiracles, with almost straight anterior margins; apices broadly pointed, posterior margins almost straight; free rear tips narrowly rounded, extending 77% (83–104%) percent of distance between pectoral and pelvic-fin bases (pectoral–pelvic space); inner margins straight to weakly convex. Pelvic fins small, with weakly convex anterior

Table 1. Morphometric data for the holotype of *Rhynchobatus springeri* sp. nov. (RMNH PISC 35839), with ranges and means for specimens <700 mm TL and >700 mm TL. Measurements are expressed as a percentage of total length.

		Paratypes (<700 mm TL) n=20			Paratypes (>700 mm TL) n=5		
	Holotype	Min.	Max.	Mean	Min.	Max.	Mean
TOT – Total length (mm)	410	374	610		748	1270	
FOR – Fork length	92.7	–	–	–	–	–	–
PCL – Precaudal length	84.1	78.9	84.5	82.4	82.1	84.6	83.9
PD2 – Pre-second dorsal length	68.6	66.7	69.3	68.2	66.6	68.7	67.6
PD1 – Pre-first dorsal length	47.3	43.9	48.1	45.6	41.5	44.5	43.4
PP2 – Prepelvic length	46.9	43.1	46.4	44.5	42.1	43.3	42.7
SVL – Snout–vent length	46.5	44.2	50.1	46.1	42.4	43.9	43.4
PSP – Prespiracular length	21.6	–	–	–	18.9	20.5	19.7
PG1 – Prebranchial length	27.3	26.1	27.4	26.8	22.8	25.4	24.1
HDL – Head length	31.5	29.2	32.6	30.9	26.8	29.5	28.5
POB – Preorbital length (direct)	17.8	15.1	17.5	16.3	12.4	15.5	14.4
POR – Preoral length	21.3	19.2	21.9	20.6	15.9	18.6	17.8
PRN – Prenarial length	15.4	13.1	15.8	14.3	11.0	14.5	12.8
IDS – Interdorsal space	15.0	14.4	16.7	15.8	15.4	18.2	16.5
DCS – Dorsal–caudal space	10.5	8.3	14.4	10.5	9.9	12.6	10.8
PPS – Pectoral–pelvic space	6.0	4.5	7.7	5.9	4.7	7.2	5.7
PCS – Pelvic–caudal space	33.9	31.2	35.7	33.6	34.4	37.8	35.3
PDS – Pelvic–dorsal space	-0.5	-0.6	1.0	0.1	-0.3	0.4	0.1
DW – Disc width	32.8	30.0	34.8	33.1	32.6	35.9	33.4
DL – Disc length	44.9	41.3	46.0	43.3	39.1	43.1	41.1
DT – Disc thickness	7.0	–	–	–	7.1	7.7	7.4
Snout – Greatest width	36.3	33.2	37.5	35.2	29.6	33.2	32.2
SWB – Snout width at base	16.2	14.9	16.5	15.8	13.6	14.8	14.3
COL – Corneal/eye length	3.3	2.3	3.2	2.7	1.5	2.1	1.8
COH – Corneal/eye height	1.8	–	–	–	1.0	1.4	1.2
EYL – Eye [eyeball] length	5.1	4.2	5.3	4.7	3.5	4.1	3.8
EYH – Eye (eyeball) height	2.3	–	–	–	2.4	2.4	2.4
INO – Interorbital space	5.6	5.0	5.7	5.2	4.6	5.2	5.0
SPL – Spiracle length	1.6	–	–	–	1.6	1.6	1.6
SPH – Spiracle height	2.4	1.8	2.5	2.2	2.0	2.2	2.1
ESL – Eye–spiracle space	6.4	–	–	–	5.2	5.2	5.2
INS – Interspiracular space	6.7	5.9	7.0	6.5	5.5	6.1	5.9
NOW – Nostril width	5.1	5.1	5.9	5.4	4.6	5.0	4.9
INW – Internarial space	4.3	3.8	4.6	4.1	3.4	3.9	3.8
ANF – Anterior nasal flap length	1.1	–	–	–	1.0	2.0	1.5
NSE – Nostril to snout edge	1.6	–	–	–	1.2	1.2	1.2
MOL – Mouth length	0.4	–	–	–	0.7	0.7	0.7
MOW – Mouth width	6.1	6.0	7.2	6.4	5.9	6.1	6.0
ULA – Upper labial furrow length	0.7	–	–	–	1.2	1.2	1.2
LLA – Lower labial furrow length	0.7	–	–	–	0.8	0.8	0.8
GS1 – First gill slit height	1.4	1.2	1.9	1.6	1.6	1.8	1.7
GS2 – Second gill slit height	1.4	1.6	1.9	1.7	1.7	1.9	1.8
GS3 – Third gill slit height	1.4	1.5	2.0	1.7	1.7	1.9	1.8

Table 1. cont'd.

		Paratypes (<700 mm TL) n=20			Paratypes (>700 mm TL) n=5		
	Holotype	Min.	Max.	Mean	Min.	Max.	Mean
GS4 – Fourth gill slit height	1.3	1.4	1.7	1.5	1.7	1.7	1.7
GS5 – Fifth gill slit height	1.1	0.9	1.4	1.2	1.0	1.3	1.1
ING1 – Inter 1st gill	14.1	12.5	15.3	14.1	12.9	14.1	13.4
ING5 – Inter 5th gill	10.4	9.8	10.6	10.2	9.6	10.4	9.9
HDH – Head height	5.2	4.1	5.0	4.7	3.8	7.5	4.8
TRH – Trunk height	7.1	3.7	8.5	7.1	8.2	9.0	8.5
TRW – Trunk width	12.6	11.8	13.9	13.2	13.6	14.3	13.9
ABH – Abdomen height	5.3	–	–	–	7.5	7.5	7.5
ABW – Abdomen width	11.0	–	–	–	12.9	12.9	12.9
CPH – Caudal peduncle height	1.6	–	–	–	1.6	1.6	1.6
CPW – Caudal peduncle width	3.2	–	–	–	3.7	4.1	3.9
VNL – Vent length	2.5	–	–	–	2.5	3.0	2.8
TFL – Tail fold length	35.1	–	–	–	34.6	35.8	35.2
P1L – Pectoral-fin length	21.9	–	–	–	20.6	22.9	21.8
P1A – Pectoral-fin anterior margin	14.2	–	–	–	13.9	15.3	14.6
P1B – Pectoral-fin base	16.4	–	–	–	16.6	17.1	16.9
P1H – Pectoral-fin height	9.0	–	–	–	10.2	10.3	10.2
P1P – Pectoral-fin posterior margin	12.3	–	–	–	12.9	15.1	14.0
P1I – Pectoral-fin inner margin	4.6	5.5	5.7	5.6	4.5	5.3	4.9
P2L – Pelvic-fin length	12.5	11.7	13.1	12.5	12.6	15.5	13.6
P2A – Pelvic-fin anterior margin	7.2	7.1	7.6	7.3	7.5	8.4	8.0
P2B – Pelvic-fin base	5.1	4.9	5.9	5.3	5.5	6.0	5.7
P2H – Pelvic-fin height	5.3	4.4	6.2	5.4	5.3	7.1	6.0
P2P – Pelvic-fin posterior margin length	8.0	–	–	–	8.4	11.9	10.2
P2I – Pelvic-fin inner margin length	7.6	6.3	8.1	7.2	7.4	10.0	8.1
P2S – Pelvic-fin span	17.0	–	–	–	19.9	19.9	19.9
CLO – Clasper outer length	–	2.0	3.0	2.6	6.5	11.5	9.4
CLI – Clasper inner length	–	–	–	–	15.7	19.9	17.8
CLB – Clasper base width	–	–	–	–	0.7	1.8	1.3
D1L – First dorsal-fin length	12.0	11.5	15.0	13.6	12.4	16.4	14.6
D1A – First dorsal-fin anterior margin	13.7	14.1	15.2	14.7	14.6	14.6	14.6
D1B – First dorsal-fin base	7.2	5.4	8.1	7.0	7.5	8.0	7.8
D1H – First dorsal-fin height	8.3	8.4	10.9	9.8	10.4	11.2	10.7
D1P – First dorsal-fin posterior margin	8.3	–	–	–	11.1	11.1	11.1
D1I – First dorsal-fin inner margin	4.8	4.9	8.8	6.6	4.9	8.4	6.5
D2L – Second dorsal-fin length	9.3	8.4	11.5	10.4	9.1	11.4	10.6
D2A – Second dorsal-fin anterior margin	10.9	10.8	10.9	10.8	11.3	11.3	11.3
D2B – Second dorsal-fin base	4.9	3.7	5.6	4.9	4.9	5.3	5.1
D2H – Second dorsal-fin height	6.1	6.1	8.1	7.0	7.1	8.9	7.9
D2P – Second dorsal-fin posterior margin	6.2	–	–	–	7.3	7.3	7.3
D2I – Second dorsal-fin inner margin	4.2	4.2	6.8	5.5	4.2	6.1	5.2
CDM – Dorsal caudal margin	15.9	14.8	17.3	15.9	15.5	17.4	16.4
CPV – Preventral caudal margin	11.1	8.8	12.0	10.6	11.0	12.4	11.6
CPL – Lower postventral caudal margin	2.9	–	–	–	3.4	3.4	3.4
CPU – Upper postventral caudal margin	9.2	–	–	–	10.3	10.3	10.3

margins, broadly pointed apices, concave posterior margins (more so anteriorly), elongate and very narrowly rounded free rear tips, and concave inner margins; inner margin very long, 1.5 (1.1–1.6) times lengths of pelvic bases; fin bases 1.2 (0.9–1.5) in pectoral–pelvic space; height of pelvic fins about 2.4 (2.1–2.9) in their lengths. Distance between pelvic-fin insertions much longer than pelvic-fin base length. Vent with well-developed folds laterally; well separated from pelvic-fin inner margins. Clasper very elongate, slender, weakly expanded distally at glans, extending almost to origin of second dorsal fin.

Vertebral column with 136 (127–139; n=30, including 8 non-types) total centra; 12 (13–19) synarcual centra, 26 (18–28) monospondylous centra, 87 (78–88) precaudal free centra, 37 (33–40) diplospondylous caudal (free) centra, 124 (113–126) free centra. Total synarcual segments 8.8% (8.8–11.6)%; monospondylous 19.1% (13.6–20.6)%; diplospondylous precaudal centra 44.9% (42.6–49.2)%, and precaudal free centra 64.0% (60.3–65.2)% of total centra count. Total pectoral radials 59–60 (57–68): 4 (1–8) free radials before propterygium, 20–21 (20–23) propterygials, 5–6 (4–5) mesopterygials, 4–5 (4–7) neopterygials, 25 (23–29) metapterygials, 55–56 (54–62) total basal radials (excluding free radials).

COLOUR.— When fresh (based on IPPS 2009–338, adult male 1126 mm TL): Dorsal surface of body pale greyish green (becoming more greenish brown well after death), with well-defined blackish pectoral spots (and dark spots and markings on orbital membranes), and a dense pattern of large, diffuse-edged white spots. Pectoral disc with narrow, weakly defined whitish border dorsally, broadest mid-anteriorly beside spiracle. Pelvic fins and clasper whitish. Orbital membrane with two curved black markings; anterior marking diverging posteriorly, abutted anteriorly by white blotch; posterior marking diverging anteriorly, larger than anterior marking, bordered ventrally by white membrane and almost abutting spiracle posteriorly; preorbit with an oblique white line (length subequal to eye diameter), directed medially. Posterior margin of spiracle and spiracular folds greyish. Black pectoral markings well defined, sharp edged, large (exceeding length of spiracle); closely surrounded by 4 white spots, lateral pair closer together than medial pair. Well defined, blackish spot posteromedial to each spiracle (diameter smaller than spiracle). White spots covering most of trunk and tail, their size subequal to pupil width or slightly smaller, bordered by faint greyish rings; in more than 3 rows on posterior part of pectoral fin; in 3–4 rows beneath first dorsal fin, spots on ventralmost row largest; in 3 well-defined, closely spaced rows along each side of tail to caudal-fin base, partly coalescing posteriorly to form a pale line; a few white spots on mid-snout and supraorbit. Ventral surface uniformly white; no irregular blackish blotch on anterior snout. In preservative (holotype): Yellowish brown above, uniformly paler yellowish white ventrally (white area appearing on tail when dry a likely

Figure 2. *Rhynchobatus springeri* sp. nov.: View of oronasal region of female holotype (RMNH PISC 35839, 410 mm TL, preserved).

Figure 3. Orbito-spiracular and scapular regions of *Rhynchobatus springeri* sp. nov, adult male paratype (IPPS 2009–338, 1126 mm TL, fresh).

artifact of preservation); unpaired fins similar to body coloration, small pale areas at base of dorsal fins. Black pectoral marking large (about ¾ orbit diameter), closely surrounded by four large, diffuse-edged white spots; two outer spots closer together than two inner spots; white spots less than half their diameter from black pectoral marking. Similar white spots present on anterior snout, interorbit, pectoral fin and in 2 main rows along side of trunk (ending beneath first dorsal fin). Orbital membrane with dark recurved markings; discontinuous, extending from near front of eye to level of spiracle; no evidence of dark postspiracular blotches. Two lines on preorbit; anterior line oblique, extending anteromedially from anteroventral edge of eye, its length slightly longer than eye; posterior line along anterior margin of orbit.

SIZE.— Females reaching at least 213 cm TL (CAS-GVF 2125 unreg); a suggested maximum size of 250–300 cm TL, based on specimens seen by one of us in Thailand (LJVC in Compagno & Last, 1999), needs confirmation; two male paratypes from Sarawak (IPPS 2009–338, adult male 1126 mm TL) and Thailand (CAS-GVF 2361 unreg) were fully mature at 113 and 125 cm TL respectively, suggesting that this species is a moderate-sized wedgefish rather than a large species.

DISTRIBUTION.— Indo–Malay region from Java (Indonesia) to Thailand, including Borneo, Singapore and the Philippines. Possibly more widespread in the Indo-Pacific, north to the East China Sea and west to Sri Lanka, but needing positive confirmation. Appears to be confined mainly to brackish coastal and estuarine habitats in shallow water.

ETYMOLOGY.—This wedgefish is named in honour of the late Stewart ("Stew") Springer who, internationally respected for his research on sharks, is hereby recognised for his contribution to the systematics of the genus *Rhynchobatus*. Vernacular: Broadnose Wedgefish.

REMARKS.— The Broadnose Wedgefish, *Rhynchobatus springeri* differs from other wedgefishes primarily in vertebral counts, but also in coloration and morphology of the snout. It has the second lowest vertebral count range of any member of the genus. Of species occurring in the region, *R. springeri* has 113–126 free vertebral centra vs. 130–139 in *R. palpebratus* (Compagno & Last, 2008), and 160–182 in *R. australiae*, 149–158 in *R.* cf. *laevis*, and 113–116 in *R.* sp. 1 (Compagno & Last, 1999). It also has a relatively broader snout than most other wedgefishes occurring in the region, with the exception of *R.* cf. *laevis*. Other species typically have either a bottle-shaped snout or the snout margin is almost straight. *Rhynchobatus* sp. 1, which has a dark body covered with large white spots, lacks a dark pectoral marking, and has rows of enlarged thorns along the rostral ridges, has characters unique within the genus. The black pectoral marking in *R. springeri* is usually surrounded by four white spots (less commonly with 3), but lacks a row of three well-defined spots adjacent its inner margin; of the other Indo–Malay species, *R. australiae* has three spots aligned in a straight row adjacent the inner margin of the pectoral marking, whereas *R. palpebratus* lacks this row of spots (also typically has four spots arranged around the pectoral marking).

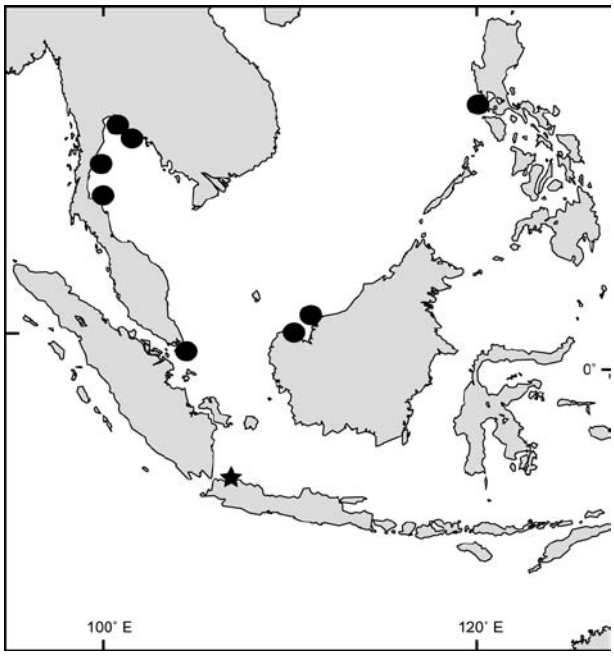

Figure 4. Distribution of *Rhynchobatus springeri* sp. nov. in the Western Central Pacific. Solid star represents holotype, solid circles represent paratypes.

Rhynchobatus springeri and *R. palpebratus* are very similar to each other. Additional to differences in vertebral counts, *R. palpebratus* has fewer, less well-developed rows of white spots along the sides of adults; the adult male holotype (CSIRO H 3384–01) of *R. palpebratus* is similar to its juvenile paratypes having two short rows of spots on each flank that terminate beneath the first dorsal fin posteriorly (the uppermost row of which sometimes continues along the mid-dorsal tail as a pale, faint line). In adult *R. springeri* (based on paratype IPPS 2009–338 and images of two discarded specimens from Sarawak), the tail is more heavily spotted, with 3–4 postdorsal rows of spots on each side that continue to the caudal fin; spots on the posterior parts of these rows sometimes coalesce to form pale lines). *Rhynchobatus springeri* also has slightly better developed thorns in the predorsal row and above the scapulocoracoid, and a marginally broader snout, but otherwise, no other obvious morphometric differences were found. However, these species have different sequences for the mitochondrial Cytochrome Oxidase 1 (COI) gene. A molecular barcode was resolved for one paratype of *R. springeri* (IPPS 2009–338, adult male 1126 mm TL) and compared with 11 *R. palpebratus* specimens (including the holotype and two paratypes).

Kimura 2-parameter corrected sequence divergence between *R. springeri* and *R. palpebratus* ranged from 2.6% to 3.0%, compared with an intraspecific range of 0.0%–0.3% for *R. palpebratus*. There may also be differences in habitat preference between these species. It appears as if *R. springeri* is found mainly in brackish coastal and estuarine waters rather than the more typical habitat of wedgefishes, the open sea; specimens observed in fish markets were associated with catches containing inshore/estuarine teleosts (e.g. *Otolithoides*, *Muraenesox* and polynemids).

The holotype of *R. springeri*, which has remained in surprisingly good condition, was collected almost a century ago from Java, eastern Indonesia. Its appearance is typical of other type specimens, although the dorsal fins (first dorsal-fin height 8.3% vs. 8.4–11.2, mean 10.0% TL) are slightly shorter than in most paratypes. Allometric patterns were not explored in the study, although changes in growth appear to be likely for some characters (see Table 1). Also, the morphometric data for the type series is more intraspecifically variable than in other rhinobatoid species. Perhaps the combination of some old and often bent material with fresh material in better condition has added unwanted variability to the data. The extent of intraspecific variability in colour and shape needs further investigation.

Compagno & Last (1999) considered *Rhynchobatus yentinensis* Wang, 1933 to be a possible synonym of their *R.* sp. 2, but later considered it more likely to be synonymous with *R. laevis* (Bloch & Schneider 1801) (Compagno & Last 2008; Eschmeyer, 2010). Wang's account of the male holotype (1010 mm TL) gives an upper tooth row count of 27 (well below the 52 rows in the holotype of *R. springeri*), a dark spot on the snout (vs. absent), first dorsal fin inserted above or slightly behind ventral-fin origin (vs. first dorsal-fin origin over pelvic-fin origin), and only 2 series of white spots (vs. 3–4 series of spots) along the tail of adult males (ca. 120 cm TL).

Comparative material.
Rhynchobatus palpebratus: CSIRO H 3384–01, adult male 1025 mm TL, north-west of Wessel Islands, Arafura Sea, Northern Territory, 10°11′ S, 137°17′ E, 50 m, 09 Feb. 1993.

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Okamejei cairae sp. nov. (Rajoidei: Rajidae), a new skate from the South China Sea

Peter R. Last[1], Fahmi[2] & Hajime Ishihara[3]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Research Centre for Oceanography, Indonesian Institute of Sciences (LIPI), Jl. Pasir Putih I, Ancol, Timur Jakarta 14430, INDONESIA
[3] W&I Associates Corporation 1020-39 Kuden, Sakae-ku, Yokohama, 247-0014, JAPAN
(Current address: PMC Amman Office, P.O. Box 144420, Amman, 11814, JORDAN)

ABSTRACT.— A new skate of the genus *Okamejei* is described from specimens collected at fish markets in Sabah, Sarawak and northwestern Kalimantan. *Okamejei cairae* sp. nov., which is presently known only from the South China Sea, has been confused in the past with a northern congener, *O. boesemani* Ishihara, from the East China Sea. These morphologically similar species share a similar coloration but *O. cairae* primarily differs from *O. boesemani* in having a smaller maximum size, smaller and fewer thorns on the disc and tail, in the numbers of predorsal vertebrae, and in some morphometric details. *Okamejei cairae* exhibits sexual dimorphism in the relative sizes of the tail, orbit, gill openings, and intergill distances and pelvic-fin base width. It is sympatric with *O. hollandi* in the South China Sea.

Key words: Rajidae – skate – new species – South China Sea – *Okamejei*

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

The genus *Okamejei* presently consists of 13 valid species (Last & Gledhill, 2008): *O. acutispina* (Ishiyama, 1958); *O. arafurensis* Last & Gledhill, 2008, *O. boesemani* (Ishihara, 1987); *O. heemstrai* (McEachran & Fechhelm, 1982); *O. hollandi* (Jordan & Richardson, 1909); *O. kenojei* (Müller & Henle, 1841); *O. leptoura* Last & Gledhill, 2008, *O. meerdervoortii* (Bleeker, 1860); *O. mengae* Jeong, Nakabo & Wu, 2007; *O. philipi* (Lloyd, 1906); *O. pita* (Fricke & Al-Hassan, 1995); *O. powelli* (Alcock, 1898); *O. schmidti* (Ishiyama, 1958). The genus is represented in the Indo–Pacific with most of these species occurring in the western North Pacific.

During various studies of the chondrichthyan faunas of the Indo–Australian Archipelago, several unidentifiable skates, including members of the genus *Okamejei*, were collected. Specimens of one of these species were included in the type series of *O. boesemani* whose type locality is from the East China Sea, west of Japan (Ishihara, 1987). These species are morphologically very similar and were only distinguished after careful examination of the more recently acquired collection material discussed below. The new species was collected in fish markets of western Borneo and caught by the Sarawak Fisheries Research vessel *KK Manchong*, during a co-funded NSF survey of the chondrichthyan parasites of Borneo and their hosts. It is described below and compared to its northern relative, *O. boesemani*.

METHODS

The descriptive format is based largely on McEachran & Fechhelm (1982), and methods follow those outlined by Last *et al*. (2008) following standards developed for skates by key researchers over the past half a century (e.g. Stehmann, 1970). Morphometric data were taken from the adult male holotype MZB 17176 and 6 paratypes (by PL, Table 1), including 2 adolescent males (CSIRO H 7099–03 and MZB 17177) and 4 females (CSIRO H 7099–01, CSIRO H 7099–02, HUMZ 37617 and HUMZ 33316); CSIRO H 7099–02 and CSIRO H 7099–06 are designated as primary female and primary juvenile paratypes respectively, in accordance with the descriptive methods given in Last *et al*. (2008). The holotype of *O. boesemani* and two other specimens were remeasured using the methods outlined above (see Table 1). All radiographs and meristic data were obtained by John Pogonoski and form part of the ANFC Skeletal Image Collection; all nine CSIRO and MZB types, and 3 HUMZ types, of the new species were radiographed. Collection acronyms follow Leviton *et al*. (1985).

Okamejei cairae sp. nov.

Figs 1–5, 6a,b, 7a, b, 8a, b; Table 1

Holotype. MZB 17176, adult male 341 mm TL, Flamboyan Market, Pontianak (West Kalimantan), Borneo, Indonesia, 00°02′ S, 109°20′ E, 12 Jul. 2008.
Paratypes. 13 specimens: CSIRO H 7099–01 (allotype), female 336 mm TL, CSIRO H 7099–02, female 353 mm TL, CSIRO H 7099–03, adolescent male 348 mm TL, CSIRO H 7099–04, adolescent male 330 mm TL, CSIRO H 7099–05, adolescent male 343 mm TL, CSIRO H 7099–06, immature male 240 mm TL, CSIRO H 7099–07, female 185 mm TL, MZB 17177, adolescent male 335 mm TL, all collected with holotype; HUMZ 33316, female 385 mm TL; HUMZ 37612, female 372 mm TL, off northwestern Borneo (Sarawak), Malaysia, 02°58′ N, 109°39′ E, 64–67 m; HUMZ 37617, female 366 mm TL; HUMZ 37629, immature male 321 mm TL, off northwestern Borneo (Sarawak) Malaysia, 03°40′ N, 109°20′ E, 80–83 m; HUMZ 37688, female 243 mm TL, off northwestern Borneo (Sarawak) Malaysia, 04°11′ N, 111°03′ E, ca 80 m.
Other material. 7 specimens: HUMZ 33375 (paratype of *O. boesemani*), adult male 355 mm TL; HUMZ 37603 (paratype of *O. boesemani*), male 306 mm TL; HUMZ 37618, female 357 mm TL; HUMZ 37633 (paratype of *O. boesemani*), male 326 mm TL; HUMZ 37661, female 369 mm TL; HUMZ 37669, female 390 mm TL; HUMZ 37670, female 374 mm TL.

DIAGNOSIS.— A relatively small species of *Okamejei* (to about 39 cm TL) with the following combination of characters: disc with narrowly rounded apices, but not especially broad, width 61–70% TL, 1.2–1.3 times its length; snout angle 87–106°; tail moderately long, length 0.9–1.1 in distance from snout tip to rear of cloaca; tail slender, width 1.2–1.7 times height at its midlength, 1.1–1.7 times at first dorsal-fin origin; pre-upper jaw length 14–16% TL, 1.8–2.1 times internasal width; ventral head length 27–30% TL; snout length 2.8–3.6 times interorbital width; orbit diameter 93–103% interorbital width in large males, 69–89% in females; first dorsal-fin height 2.3–3.0 in its base length; distance from first dorsal-fin origin to tail tip 4.1–5.4 times first dorsal-fin base length, 2.9–3.2 times caudal-fin length; pelvic fins of medium size, length of posterior lobe 15–17% TL, length of anterior lobe 78–92% of posterior lobe; adult clasper about 22% TL, connected to pelvic-fin inner margin at about 40% of its length from cloaca in adult male; clasper glans expanded slightly, funnel soft, claw-like; anterior margins of both surfaces of disc of males with denticle bands, dorsal bands absent in females and juveniles; 1–3 nuchal thorns present; malar thorn patch elongate, posteriorly positioned; tail thorns very small (rudimentary and possibly deciduous in mature males), in 5 irregular rows in both sexes and juveniles; total pectoral radials 78–84; trunk centra 24–31; predorsal centra 68–75; total centra 123–141; tooth rows in upper jaw 40–51; mainly yellowish to brownish with variable size clusters of fine brownish spots (sometimes faint) over most of dorsal disc; rostral cartilage not strongly demarcated from rest of snout; prominent, dark brown ocellate markings near rear tip, and often near centre, of each pectoral fin; ventral surface usually pale to medium greyish brown over head and abdomen, distinctly darker than paler area around outer margin of disc; ventral sensory pores large, silvery white with dark margins when fresh, becoming uniformly black in preservative, not surrounded by greyish blotches, absent from abdomen and pelvic girdle; each dorsal fin with a dark anterior saddle, caudal fin with two dark bars.

DESCRIPTION.— Disc weakly quadrangular, 1.16 times as broad as long in 341 mm TL adult male holotype (1.18 times in 2 adolescent male paratypes, 335–348 mm TL; 1.18–1.30 times in 4 female paratypes, 336–385 mm TL); angle in front of orbits 86° (87–90°; 96–106°); axis of greatest width 58% (53–59%; 53–56%) of disc length; anterior margin weakly double concave (usually less pronounced in females and juveniles), strongly concave anteriorly toward snout apex, moderately convex beside and slightly forward of eyes, weakly concave beside spiracles; apex very narrowly rounded to bluntly pointed; posterior margin moderately convex; free rear tip very broadly rounded. Head relatively short, preorbital snout length 3.47 (3.71–3.90; 3.71–4.70) times orbit length, 3.58 (3.54–3.61; 2.79–3.60) times interorbit; pre-upper jaw length 2.01 (1.94–2.00; 1.83–2.07) times internarial distance. Snout tip well produced, prominent, narrowly pointed (more so in adult males; quite short in female allotype CSIRO H 7099–01; no fleshy process at apex. Orbit diameter 1.03 (0.93–0.96; 0.69–0.89) times interorbital width. Spiracle small, length 2.12 (2.14–2.23; 1.31–1.89) in orbit diameter; opening teardrop-shaped to suboval. Nostril broadly suboval, usually distorted; anterior nasal flap expanded slightly, its lateral margin somewhat tubular, its anterior margin weakly lobe-like and mostly concealed beneath nasal curtain, its posterior inner margin barely concealed by nasal curtain; posterior lobes well developed, forming nasal curtain, produced posterolaterally and narrowly rounded apically, posterolateral margins with long fringe; internarial distance 1.87 (1.76–1.85; 1.85–1.99) in distance between first gill slits, 0.93 (0.91–0.95; 1.00–1.09) in distance between fifth gill slits. Upper jaw moderately arched in both sexes (less so in smallest paratypes), not indented at symphysis; lower jaw not angular, not double convex; jaws; lateral teeth not usually concealed by lobe of nasal curtain. Teeth of adult male holotype strongly unicuspid with raised subcircular bases in middle of jaws; arranged in obvious longitudinal rows; main cusps elongate, slender, tips blunt to pointed, posteriorly directed in upper jaw; cusps shorter, broader, blunt laterally; central cusps of adolescent males more developed than females but less so than adult male holotype. Teeth of females and juveniles in quincunx, with broad oval crowns, cusps very short (relatively well developed in juveniles).

Figure 1. *Okamejei cairae* sp. nov., adult male holotype (MZB 17176, 341 mm TL, fresh): A. dorsal surface; B. ventral surface.

Table 1. Morphometrics for the adult male holotype of *Okamejei cairae* sp. nov. (MZB 17176) and ranges for the 6 measured paratypes, as well as remeasured values for the adult male holotype (MTUF 25916) and two other female specimens of *O. boesemani*. Values are expressed as percentages of total length (TL).

	Okamejei cairae sp. nov.							*Okamejei boesemani*			
		Paratypes						Other material			
		Males (n=2)			Females (n=4)			Females (n=2)			
	Holotype	Min.	Max.	Mean	Min.	Max.	Mean	Holotype	Min.	Max.	Mean
Total length (mm)	341	335	348	–	336	385	–	464	513	529	
Disc width	60.6	61.6	62.6	62.1	64.3	69.6	67.1	67.0	70.1	70.6	70.3
Disc length (dir)	52.3	52.4	53.0	52.7	53.7	55.8	54.8	56.4	58.2	58.4	58.3
Snout to maximum width	30.5	28.3	30.9	29.6	28.5	31.1	29.6	30.9	31.0	32.1	31.6
Snout length (preorbital) - dir	13.6	14.5	14.7	14.6	13.5	15.8	15.0	15.1	16.2	16.7	16.5
Snout to spiracle	18.6	19.5	19.8	19.6	18.8	20.8	20.0	19.8	21.0	21.5	21.3
Head - dorsal	19.8	20.8	20.9	20.8	20.2	22.2	21.4	21.6	22.4	23.0	22.7
Orbit diameter	3.9	3.8	3.9	3.8	3.4	3.7	3.6	3.5	3.1	3.4	3.2
Orbit and spiracle length	5.2	5.3	5.3	5.3	4.8	5.4	5.1	4.8	4.7	4.9	4.8
Spiracle length - main pore	1.9	1.7	1.8	1.8	1.9	2.8	2.3	1.6	1.7	2.1	1.9
Distance between orbits	3.8	4.1	4.1	4.1	4.2	4.9	4.7	4.4	5.2	5.2	5.2
Distance between spiracles	5.4	5.7	5.8	5.8	5.9	6.6	6.2	6.5	6.3	6.5	6.4
Distance-snout to cloaca	47.5	48.0	48.5	48.2	49.5	51.9	50.4	50.9	51.9	52.0	51.9
Cloaca to D1	28.8	28.9	30.3	29.6	24.1	27.4	26.2	25.7	23.7	23.9	23.8
Cloaca to D2	37.6	37.8	38.4	38.1	34.4	35.7	35.0	34.4	32.1	33.0	32.5
Cloaca to caudal origin	43.7	43.5	43.8	43.6	40.1	43.0	41.6	41.2	37.4	39.4	38.4
Distance-cloaca to caudal fin tip	52.5	51.5	52.0	51.8	46.8	50.5	48.9	49.1	44.6	45.2	44.9
Snout length (pre upper jaw)	14.0	13.9	14.6	14.2	13.5	15.5	14.7	14.4	15.3	16.4	15.9
Prenasal length	10.9	11.3	12.0	11.6	10.8	12.4	12.0	11.8	12.6	13.9	13.2
Head length to fifth gill	27.8	27.2	28.0	27.6	28.1	30.1	29.0	29.2	30.0	30.4	30.2
Mouth width	7.7	7.6	7.9	7.8	7.5	8.1	7.8	7.8	7.2	8.0	7.6
Distance between nostrils	7.0	7.2	7.3	7.2	7.3	7.5	7.4	7.6	7.3	7.4	7.4
Nasal curtain-length	4.8	4.8	4.9	4.8	4.0	4.9	4.5	4.7	4.7	5.0	4.8
Nasal curtain-total width	9.2	8.3	8.7	8.5	8.8	9.2	9.0	8.8	8.5	8.7	8.6
Nasal curtain - min width	5.8	5.2	5.5	5.4	5.8	6.5	6.0	6.2	5.7	6.0	5.8
Nasal curtain - lobe width	1.8	1.3	1.6	1.4	1.4	1.9	1.6	1.5	1.9	2.0	1.9
Width of 1st gill opening	1.5	1.4	1.5	1.4	1.7	2.2	1.9	1.3	1.7	1.8	1.8
Width of 5th gill opening	1.1	1.0	1.2	1.1	1.4	1.6	1.5	1.2	1.2	1.4	1.3
Distance between 1st gill openings	13.0	12.8	13.2	13.0	13.9	14.7	14.3	14.3	14.6	15.3	14.9
Distance between 5th gill openings	6.5	6.6	6.8	6.7	7.3	8.2	7.8	7.9	8.4	8.6	8.5
Clasper-postcloacal length	22.2	15.8	18.2	17.0	–	–	–	22.4	–	–	–
Length of anterior pelvic lobe	13.1	12.9	12.9	12.9	12.3	13.4	12.9	12.6	14.6	15.0	14.8
Length of posterior pelvic lobe	16.9	15.4	16.3	15.9	14.6	15.5	15.0	19.5	17.1	17.5	17.3
Pelvic base - width	8.0	7.6	8.6	8.1	9.1	10.4	9.9	7.5	10.0	10.5	10.2
Tail at axil pelvic fins - width	3.4	2.6	3.1	2.8	2.7	3.4	3.1	3.5	4.0	4.3	4.1
Tail at axil pelvic fins - height	1.7	1.7	1.8	1.8	1.8	2.1	1.9	1.8	2.0	2.1	2.1
Tail at midlength - width	1.8	1.6	1.7	1.6	1.2	1.8	1.6	2.1	2.2	2.2	2.2
Tail at midlength - height	1.1	1.1	1.1	1.1	1.0	1.4	1.2	1.1	1.1	1.2	1.1
Tail at D1 origin - width	1.6	1.6	1.6	1.6	1.4	1.7	1.6	2.0	2.1	2.2	2.2
Tail at D1 origin - height	1.1	1.0	1.0	1.0	1.2	1.2	1.2	1.2	1.1	1.2	1.2
D1 base - length	5.5	4.8	4.8	4.8	4.5	5.4	5.0	5.6	5.1	5.4	5.3
D1 - height	2.2	1.7	1.8	1.8	1.6	1.9	1.8	2.8	1.6	2.0	1.8
D1 orig to caudal fin tip	22.8	21.5	22.3	21.9	20.4	26.2	22.9	23.5	20.6	22.0	21.3
D2 orig to caudal fin tip	14.3	13.1	13.7	13.4	12.2	15.6	13.9	14.5	11.7	13.2	12.4
Caudal-fin length	7.4	7.0	7.5	7.3	6.4	7.0	6.7	7.5	5.2	7.9	6.6
Interdorsal space	3.0	3.0	4.4	3.7	2.9	5.7	4.3	3.2	3.3	3.4	3.3

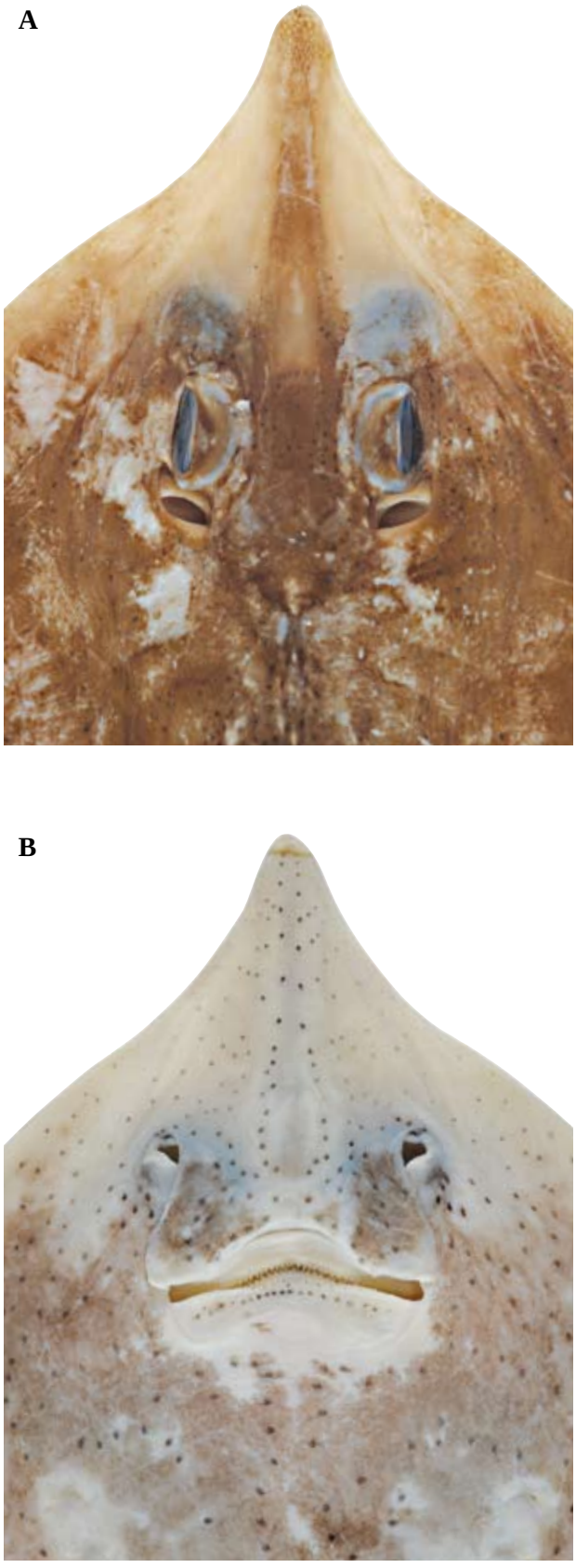

Figure 2. *Okamejei cairae* sp. nov., adult male holotype (MZB 17176, 341 mm TL, preserved): A. dorsal head; B. ventral head.

Pelvic fins deeply forked; anterior lobe short, mainly slender, lateral margin entire, distal and inner margins deeply incised; posterior lobe very elongate 16.9% (15.4–16.3%; 14.6–15.5%) TL, lateral margins serrate, straight to weakly convex (more convex in females and juveniles), free rear tip narrowly rounded (usually angular in females and juveniles); inner margin usually straight, connected to anterior lateral margin of clasper at about 40% of adult postcloacal length; anterior lobe 0.78 (0.79–0.84; 0.83–0.92) times posterior lobe. Clasper moderately elongate, about 22% TL, slender, depressed, glans expanded slightly; clasper components include proximal and distal clefts, terminal bridge, pseudorhipidion, rhipidion, shield, sentinel, spike and funnel; denticles and pseudosiphon absent. Tail very slender, slightly depressed; relatively narrow at base, barely tapering from its base, tapering gradually to tail tip beyond second dorsal fin; not expanded at its midlength; width at insertions of pelvic fins 1.88 (1.61–1.87; 1.80–2.27) times width at midlength of tail and 2.11 (1.58–1.93; 1.74–2.41) times width at first dorsal-fin origin respectively; length from rear of cloaca 1.10 (1.06–1.08; 0.90–1.02) times distance from tip of snout to rear of cloaca; anterior cross-section suboval, not more convex on dorsal surface than ventral surface posteriorly, almost flat ventrally near tail apex; width 1.93 (1.39–1.80; 1.49–1.68) times height at insertion of pelvic fin, 1.69 (1.48–1.54; 1.19–1.33) times height at midlength, 1.50 (1.54–1.68; 1.14–1.45) times height at first dorsal fin origin; lateral tail fold very poorly developed, very narrow and not obvious for most of its length, its origin obscure (usually near first dorsal fin); fold obscure at tail tip. Dorsal fins small, of similar shape and size (first dorsal fin not taller and not more upright than second); first dorsal-fin height 2.46 (2.65–2.79; 2.30–2.98) in base length; fins low, rounded, very strongly raked, elongate with very short bases; anterior margins weakly convex, apices broadly rounded, posterior margins short, convex, inner margins short; interdorsal distance very long, 1.84 (1.09–1.61; 0.85–1.88) in length of first dorsal-fin base; distance from first dorsal-fin origin to tail tip 4.16 (4.47–4.63; 4.07–5.37) times dorsal-fin base length, 3.08 (2.86–3.18; 2.92–3.44) times caudal-fin length; first dorsal-fin base 0.74 (0.64–0.69; 0.64–0.85) times caudal-fin length. Epichordal caudal-fin lobe very well developed, very long-based, tall, its height subequal to tail width at its origin; usually tallest near its midlength; pointed or truncate distally, its posterodorsal margin usually straight, often irregular; usually connected to second dorsal fin by low ridge; hypochordal caudal lobe vestigial.

Dorsal surface of adult male holotype with very small to rudimentary orbital, nuchal, malar and tail thorns, alar thorns larger; thorns around orbit and on tail delicate, deciduous; female allotype CSIRO H 7099–02 (353 mm TL) with small orbital and tail thorns; primary juvenile paratype CSIRO H 7099–06 (240 mm TL, male) with poorly developed thorns. Orbital thorns of holotype feeble, minute to very small, many missing (probably

Figure 3. *Okamejei cairae* sp. nov., female allotype (CSIRO H 7099–02, 353 mm TL, fresh): dorsal surface.

deciduous, missing thorns evidenced by naked skin pockets), forming a disjunct rosette; 7 when intact (2 on preorbit, 2 on midorbit, 3 on postorbit); strongly tilted, directed posteriorly. Female allotype with better developed orbital thorns than holotype, 11 (3 on preorbit, 5 on midorbit, 3 on postorbit); thorns oblique, continuous, last postorbital thorn near posterior margin of spiracle; primary juvenile with 7 small, oblique thorns (2 on preorbit, 3 on midorbit, 2 on postorbit). Nuchal thorns of holotype 3, short, strongly tilted, bases raised slightly; similar in female allotype, 3 thorns; single thorn in primary juvenile. Malar patch with about 20 enlarged, semi-prostate thorns in about 1–2 poorly defined rows; main patch very elongate, not curved, located along disc margin, commencing beside eye and extending for length equivalent to prenasal distance; malar thorns similar in size and appearance to alar thorns; malar thorns merging with a patch of smaller more upright thornlets and denticles laterally, and anteriorly and posteriorly. Alar patch of holotype about 27 thorns in about 2 rows; thorns much larger than median thorns, partly embedded, prostrate, not retractable; thorns undulate, directed posteromedially, with pungent barbed or spear-shaped tips; patch narrow, only slightly longer than length of malar patch. Tail thorns in adult male holotype very poorly developed, rudimentary or missing, 5 incomplete and indistinct rows; about 7 remaining (several lost) predorsal median thorns, smaller than nuchal thorns; interdorsal thorns 5, minute; about 5-10 remaining thorns in each of the dorsolateral and lateral rows; tail abraded so most of these feeble thorns may have been lost. Female allotype with 5 irregular rows of small, strongly oblique tail thorns, these rows not developed equally; median row originating just behind level of cloaca, thorns variable in size, about 26 predorsally (15 main thorns and 11 very small thornlets), better developed than lateral rows; interdorsal thorns 10; dorsolateral rows semi-continuous (20–22 thorns) with larger thorns than lateral rows (19–24, mostly thornlets); some minute thornlets on lateral tail posterior of first dorsal fin. Primary juvenile paratype with median row best developed, thorns small, oblique (11 in row); interdorsal thorns 1; all lateral thorns present as minute, embedded thornlets (about 9–12 dorsolaterally, 4–5 laterally).

Denticles of adults poorly developed, most of dorsal disc and tail naked. In adult male holotype, dorsally confined to snout tip and anterior disc margin (commencing above tip of propterygium and extending almost to pectoral apex); ventrally, in a narrow band along snout margin forward of nostrils. In female allotype, dorsally confined to snout tip; ventrally, in a short, narrow band along snout margin forward of nostrils; primary juvenile entirely naked.

Meristics (n=12): Tooth rows in upper jaw 44 in holotype (40–51 in paratypes); lower jaw 41 (37–51). Pectoral-fin propterygial radials 31–32 (29–34); mesopterygial radials 14–15 (13–17); metapterygial radials 35–36 (33–35); total radials 81–82 (78–84). Pelvic-fin radials mature and adolescent males (n=6) 1 (1) + 19 (18–20); females (n=5) (1) + (19–21). Trunk centra 28 (24–31); predorsal caudal centra 44 (37–47); predorsal centra 72 (68–75); centra between origins of dorsal fins 16 (14–20); diplospondylous centra 110 (95–113); total centra about 138 (123–141).

COLORATION (fresh).— In holotype: Dorsal surface of disc, pelvic fins, claspers and tail brownish, somewhat blotched; only slightly paler on snout and around margins of disc; skin above rostral cartilage barely demarcated from rest of snout; dense clusters of small brownish dot-like markings over most of dorsal surface; spots notably absent from posterior outer disc, snout, anterior lobe of pelvic fin, orbital membranes and claspers; a prominent dark brown ocellus (of similar size to orbit) near rear tip of each pectoral fin; a slight larger pair of dotted ocelli near centre of each pectoral fin; eyes dark; dorsal fins brownish, each with a dark, anteriorly positioned, basal saddle (forming an elongate bar in some paratypes); caudal fin with two dark brown bars (one positioned apically, the other well behind fin origin). Ventral surface greyish brown and white; dark areas around posterior head, over abdomen, around cloaca and along tail; whitish or translucent areas mainly on prenasal snout, outer disc and claspers; smaller pale patches on chin and around gill slits; sensory pores large, rather sparse, silvery white with dark margins (becoming uniformly blackish in preservative), not surrounded by greyish blotches; absent on abdomen, pelvic girdle and most of outer posterior disc. Paratypes: similar to holotype, dorsal base coloration varying from yellowish to brownish; positions of dot-like clusters and development of ocelli differ between individuals; posterior ocelli (incomplete or as a solid ring) usually more obvious than mid-pectoral ocelli; dark areas on ventral surface more extensive in some paratypes than holotype. In preservative: Similar to fresh coloration, usually with less obvious clusters of spots on dorsal surface; ventral pores black and strongly contrasted against pale ventral disc.

Figure 4. Orbito-spiracular region of *Okamejei cairae* sp. nov., female allotype (CSIRO H 7099–02, 353 mm TL, preserved) showing the relative sizes and positions of the spiracle and orbit and their associated thorns.

Figure 5. Oronasal region of *Okamejei cairae* sp. nov., female allotype (CSIRO H 7099–02, 353 mm TL, fresh).

SIZE.— Females to at least 390 mm TL; males adolescent at about 330–348 mm TL, fully mature at 341–355 mm TL, males probably smaller than females.

DISTRIBUTION.— Off western Borneo in the South China Sea. Specific localities mostly unknown but collected in fish markets of Sabah, Sarawak, and northwestern Kalimantan (Pontianak). Depth range not well defined, but probably mainly on the mid continental shelf (ca 65–150 m).

ETYMOLOGY.— The epithet *cairae* recognises the major contribution made to our knowledge of sharks and rays of the world by Connecticut-based parasitologist, Dr Janine Caira, during her quest to describe the metazoan parasite faunas of these animals. During extensive field surveys to remote regions, including all parts of coastal Borneo, Dr Caira gained an excellent knowledge of the taxonomy of the host fauna as well as their parasites. She also co-ordinated the collection of important chondrichthyan material during these surveys in Borneo, and was fortuitously present at the central market in Pontianak, Kalimantan, when a large collection of this species, including most of the type series, was made. Proposed vernacular name: ‘Borneo Sand Skate’.

REMARKS.— Based on Ishihara’s (1987) revision of Western North Pacific *Okamejei*, *O. cairae* most closely conforms to *O. boesemani*; to such an extent that specimens of both species were included in the type series of the latter. However, the species differ primarily

in maximum size, squamation, and meristic data and some morphometric details. *Okamejei boesemani* (Fig. 9) appears to be a larger skate (attaining at least 47 cm, possibly 52 cm TL; male HUMZ 94846 still immature at 40 cm TL) than *O. cairae* (females to 39 cm TL; males adolescent at 33–34 cm TL, n=3). The tail thorns of *O. cairae* are much more reduced in size than those of *O. boesemani* but occur in more rows. Also, based on material examined, *Okamejei cairae* has more vertebrae: predorsal centra 68–75 (mean 70.8, n=12) versus 63–66 (mean 64.3, n=3); these data are in agreement with data provided by Ishihara (1987) for the holotype of *O. boesemani* (65) from the East China Sea, and the three paratypes (HUMZ 33375, 37603, 37633), presumably of *O. cairae* (70–76), from the southern sector of the South China Sea. Relative to its total length, *O. cairae* appears to have: a larger orbit (diameter in males 3.8–3.9 versus 3.5% TL in male holotype of *O. boesemani*, 3.4–3.7 versus 3.1–3.4% TL in females of *O. boesemani*) and combined orbit and spiracle length (4.8–5.4 versus 4.7–4.9% TL in both sexes); longer tail (length in males 51.5–52.5 versus 49.1% TL in male holotype of *O. boesemani*, 46.8–50.5 versus 44.6–45.2% TL in females of *O. boesemani*)

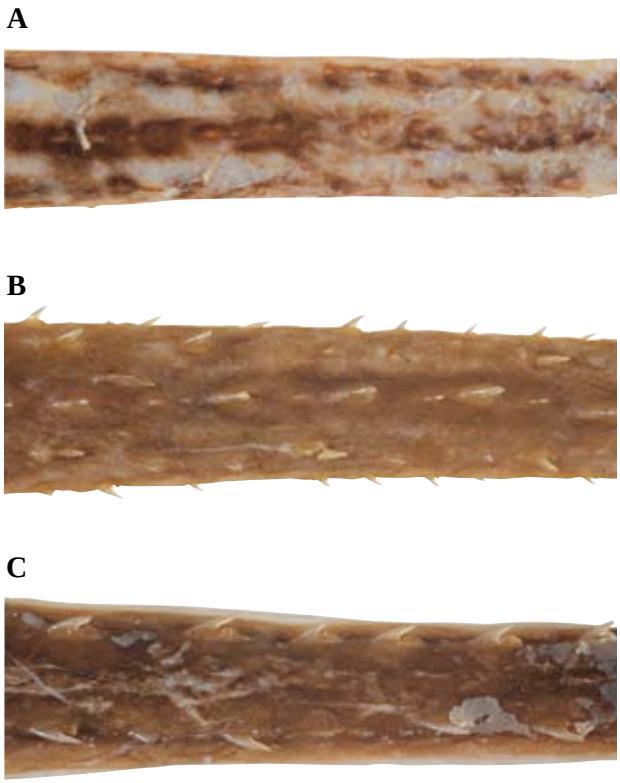

Figure 6. Dorsal view of the mid tail of *Okamejei* species: A. adult male holotype (MZB 17176, 341 mm TL, preserved) *O. cairae* sp. nov.; B. female allotype (CSIRO H 7099–02, 353 mm TL, preserved) *O. cairae* sp. nov.; C. immature male (HUMZ 94846, 397 mm TL, preserved) *O. boesemani*.

Figure 7. Lateral view of the mid tail of *Okamejei* species: A. adult male holotype (MZB 17176, 341 mm TL, preserved) *O. cairae* sp. nov.; B. female allotype (CSIRO H 7099–02, 353 mm TL, preserved) *O. cairae* sp. nov.; C. immature male (HUMZ 94846, 397 mm TL, preserved) *O. boesemani*.

and associated predorsal distances; smaller disc (width 60.6–62.6 versus 67% TL in male, 64.3–69.6 versus 70.1–70.6% TL in females; disc length 52.3–53.0 versus 56.4% TL in male, 53.7–55.8 versus 58.2–58.4% TL in females); narrower interorbit (width 3.8–4.1 versus 4.4% TL in male, 4.2–4.9 versus about 5.2% TL in females); and a slightly shorter preorbital snout (width 13.6–14.7 versus 15.1% TL in male, 13.5–15.8 versus about 16.2–16.7% TL in females).

Like most other skates, *Okamejei cairae* is sexually dimorphic with respect to the morphometrics, differing greatly in two non-standard ratios: orbit diameter 2.12–2.23 (mean 2.16) times spiracle opening in males versus 1.31–1.88 (1.58) in females; tail width at midlength 1.48–1.69 (1.57) times its height in males versus 1.19–1.33 (1.27) in females. Other differences include: a longer tail and relatively smaller disc in males (disc width 60.6–62.6 versus 64.3–69.6% TL; disc length 52.3–53.0 versus 53.7–55.8% TL); smaller gill openings and intergill distances in males (width of 1st gill opening 1.4–1.5 versus 1.7–2.2% TL; width of 5th gill opening 1.0–1.2 versus 1.4–1.6% TL; distance between 1st gills 12.8–13.2 versus 13.9–14.7% TL; distance between 5th gills 6.5–6.8 versus 7.3–8.2% TL); a narrower pelvic base in males (width 7.6–8.6 versus 9.1–10.4% TL); and a larger orbit in males (diameter 3.8–3.9 versus 3.4–3.7% TL).

Okamejei cairae is taken sympatrically with *O. hollandi* (Fig. 10) off western Borneo. While similar in meristics, *O. hollandi* differs markedly from the new species at the ND2 gene (G. Naylor, pers. comm.), and by having larger

Figure 8. Lateral view of the posterior fins of *Okamejei* species: A. adult male holotype (MZB 17176, 341 mm TL, preserved) *O. cairae* sp. nov.; B. female allotype (CSIRO H 7099–02, 353 mm TL, preserved) *O. cairae* sp. nov.; C. immature male (HUMZ 94846, 397 mm TL, preserved) *O. boesemani*.

tail thorns, generally more widely spaced dorsal fins, a dense pattern of blackish flecks distributed uniformly over the dorsal disc (rather than in clusters), and a darker ventral surface; no information presently exists for the ND2 gene of *O. boesemani*.

Also, the pectoral axil marking is a brown pale-edged blotch rather than a dark brown ocellus. In addition, *O. hollandi* may mature at a smaller size: CSIRO H 7099–08 mature at 311 mm TL vs. 341 mm TL for smallest adult male of *O. cairae*.

Two specimens, taken by the *KK Manchong* off Sarawak and most closely identifiable to *O. cairae* (BO 410, BO 411), were excluded from the type series as they are considerably larger (403–451 mm TL) with a paler dorsal disc and more striking colour pattern than members of the type series of *O. cairae*. These specimens require further investigation.

Comparative material.
Okamejei boesemani: MTUF 25916 (holotype), adult male 464 mm TL; HUMZ 33681, female 513 mm TL; HUMZ 34848, female 529 mm TL; HUMZ 108658, female size not recorded; HUMZ 94846, immature male 397 mm TL; HUMZ 34880, female 515 mm TL.
Okamejei cf. *cairae*: NSFEP BO 410, female 451 mm TL; NSFEP BO 411, female 403 mm TL.
Okamejei hollandi: HUMZ 109133, immature male 246 mm TL; HUMZ 109134, female 358 mm TL; CSIRO H 7099–08 (formerly KA 337), adult male 311 mm TL; and 14 unregistered specimens taken by the NSF parasite project.

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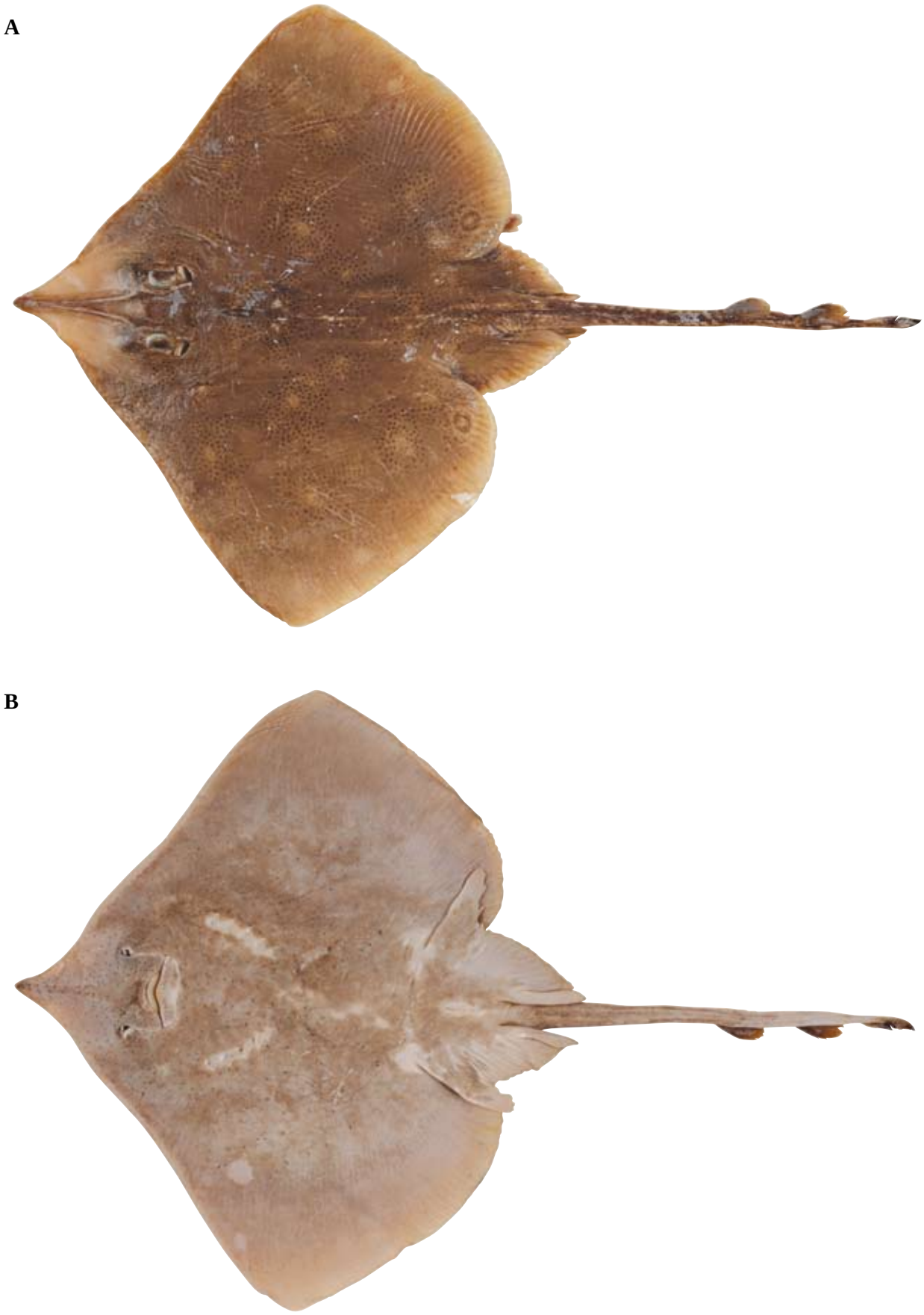

Figure 9. *Okamejei boesemani*, immature male (HUMZ 94846, 397 mm TL, preserved): A. dorsal surface; B. ventral surface.

Figure 10. *Okamejei hollandi*, adult male (CSIRO H 7099–08, 311 mm TL, fresh): A. dorsal surface; B. ventral surface.

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A new species of skate *Okamejei jensenae* sp. nov. (Rajoidei: Rajidae) from the seas off Borneo, with a redescription of the Kwangtung Skate, *Dipturus kwangtungensis* (Chu)

Peter R. Last[1] & Annie P.K. Lim[2]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Fisheries Biosecurity Centre Sarawak, Jalan Buruh, 93450, Kuching, Sarawak, MALAYSIA

ABSTRACT.— A new species of skate of the genus *Okamejei* is described based on specimens collected from the Sulu Sea off Malaysian Borneo and the Philippines. *Okamejei jensenae* sp. nov. can be distinguished from other members of the genus found in this region by a combination of coloration, squamation, morphometrics and meristics. Another rajid skate, *Dipturus kwangtungensis* (Chu), newly collected from the southern South China Sea, off western Borneo, is redescribed based on material collected by the Fisheries Research Institute, Sarawak. This species is frequently confused in the literature with other species of *Dipturus* found in the western North Pacific.

Key words: Rajidae – skate – new species – Borneo – *Okamejei jensenae* – *Dipturus kwangtungensis*

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

The rajid genus *Okamejei* presently consists of 14 valid species, including a new species described earlier in this publication (Last *et al*., 2010) from off western Borneo, in the South China Sea. Three members of the genus are known to occur in the seas off Borneo: *O. cairai* Last, Fahmi & Ishihara, 2010, *O. hollandi* (Jordan & Richardson, 1909) and another new skate described herein. The new skate is known only from the Sulu Sea, from where the first specimens were taken during a survey of the elasmobranchs of the Philippines in the 1990s (Compagno *et al*., 2005).

During recent fisheries surveys off Borneo, a fourth rajid skate belonging to the genus *Dipturus* was collected. This skate, *Dipturus kwangtungensis* (Chu, 1960), was originally described from three specimens (SFI 57–0676, SFI 57–0674, SFI 57–0675) collected off Chapo (Hailing Tao) in the northern South China Sea. Ishiyama (1967) provided a full translation of Chu's (1962) brief Chinese redescription of the species into English. In his review of the genus *Raja* (now including elevated subgenera, *Dipturus* and *Okamejei*), Ishihara (1987) provided a lengthy treatment of this species based on the types and additional material collected from off Japan. However, after a close inspection of images and data presented in his redescription and diagnosis, we have concluded that Ishihara's materials contain more than a single species. Hence, some character states defining the species are confused and these circumstances may have contributed to subsequent misidentifications of the species in the literature. A redescription of this species is provided based on two new specimens from the South China Sea, and compared to data presented by Ishihara (1987).

METHODS

The descriptive format follows other recent skate manuscripts and is based on McEachran & Fechhelm (1982), and closely follows methods outlined by Last *et al*. (2008). Morphometric data for the new *Okamejei* species were taken from the female holotype (PNM 15096), three female paratypes (CSIRO H 7111–01, SUML F 1136 and IPPS 2010–03), and a non-type specimen (field number JPAG 328 of unknown whereabouts); the holotype and paratypes were radiographed to obtain meristic details). Two specimens of *Dipturus kwangtungensis* (IPPS 2010–01 and CSIRO H 7100–01) from Borneo were used to obtain morphometric and meristic information; these were compared to data published by Ishihara (1987). All radiographs and meristic data for this study were obtained by John Pogonoski, manager of the ANFC Skeletal Image Collection. Key collection acronyms follow Leviton *et al*. (1985) with the following additions or changes: Australian National Fish Collection, Hobart, Australia (CSIRO); Institut Penyelidikan Perikanan

Sarawak/Sarawak Fisheries Research Institute, Kuching, Malaysia (IPPS). Specimens collected in the Philippines as part of a WWF-funded project are deposited as the Silliman University Marine Laboratories (SUML) and unregistered specimens from this project are prefixed with the acronyms JPAG or BRU.

Okamejei jensenae sp. nov.

Figs 1–6; Table 1

Okamejei sp. 1: Compagno *et al*., 2005, 68.

Holotype. PNM 15096 (formerly SUML F 1135), female 488 mm TL, Dipolog Public Market, Dipolog City, Philippines, ca. 08°28′ N, 123°20′ E, 08 Apr. 1999.
Paratypes. 3 specimens: CSIRO H 7111–01 (formerly BRU 169), female 464 mm TL, Palapala, Cadiz City, Philippines, 10°57′ N, 123°18′ E, 06 Apr. 2000; IPPS 2010–03, female 496 mm TL, Sulu Sea, Malaysia, 04°45.90′ N, 118°47.95′ E, 110–118 , 30 Jul. 2009; SUML F 1136, female 518 mm TL, collected with the holotype.
Other material. 5 specimens: SUML unreg (JPAG 328), female 533 mm TL, Cebu Fish Port, Cebu City, Philippines; SUML unreg (BRU 167), female 340 mm disc width, SUML unreg (BRU 168), female 315 mm disc width, SUML unreg (BRU 170), female 335 mm disc width, SUML unreg (BRU 172), immature male 240 mm disc width, Palapala, Cadiz City, Philippines. The whereabouts of these specimens, identified by Peter Last and John Stevens at SUML in May 2000, is presently unknown.

DIAGNOSIS.— A medium-sized species of *Okamejei* (to about 53 cm TL) with the following combination of characters: disc with broadly rounded apices, width 65–71% TL, about 1.2 times its length; snout angle 95–98°; tail relatively short, length 0.8–0.9 in distance from snout tip to rear of cloaca; tail width 1.6–1.8 times height at its midlength, 1.5–1.7 times at first dorsal-fin origin; pre-upper jaw length 17–18% TL, 2.0–2.2 times internasal width; ventral head length 30–32% TL; snout length 3.3–3.4 times interorbital width; orbit diameter 67–84% interorbital width in females; first dorsal-fin height 2.0–2.6 in its base length; distance from first dorsal-fin origin to tail tip 3.1–3.6 times first dorsal-fin base length, 3.4–6.3 times caudal-fin length; pelvic fins of medium size, length of posterior lobe 16–18% TL, length of anterior lobe 75–83% of posterior lobe; adult clasper unknown; anterior margins of both surfaces of disc of females with denticle bands; nuchal thorns forming part of long series of thorns extending along midline of disc; tail thorns well developed, numerous, concentrated into multiple rows along middle and lateral tail, absent from dorsolateral region; total pectoral radials 80–82; trunk centra 26–31; predorsal centra 79–85; total centra 133–138; tooth rows in upper jaw 61–76; brownish and white spotted, with large dark pectoral spots bordered with smaller white spots when fresh (spotting sometimes obscure in preservative); rostral cartilage usually demarcated from rest of snout; ventral surface mostly white with outer margins of pectoral fins yellowish; ventral sensory pores minute, indistinct, not surrounded by greyish blotches; dorsal fins dark anteriorly, paler posteriorly; caudal fin pale.

DESCRIPTION.— Disc weakly quadrangular, 1.15 times as broad as long in 488 mm TL female holotype (1.15–1.18 times in the 3 paratypes and one other measured specimen, SUML unreg. JPAG 328); angle in front of orbits 98° (95–96°); axis of greatest width 56% (52–58%) of disc length; anterior margin weakly double concave, more strongly concave anteriorly toward snout apex, moderately convex beside and slightly forward of eyes, weakly concave beside spiracles; apex broadly rounded; posterior margin moderately convex; free rear tip broadly rounded. Head relatively short, preorbital snout length 4.72 (4.01–4.99) times orbit length, 3.35 (3.32–3.37) times interorbit; pre-upper jaw length 2.09 (1.98–2.23) times internarial distance. Snout tip produced slightly, prominent, narrowly pointed, no fleshy process at apex. Orbit diameter 0.71 (0.67–0.84) times interorbital width. Spiracle small, length 1.23 (1.18–1.61) in orbit diameter; opening suboval. Nostril broadly suboval, usually distorted; anterior nasal flap barely expanded, its lateral margin weakly tubular, its anterior margin weak and partly concealed beneath nasal curtain, its posterior inner margin not concealed by nasal curtain; posterior lobes well developed, forming nasal curtain, produced posterolaterally and broadly rounded apically, posterolateral margin with obvious fringe; internarial distance 2.06 (2.00–2.17) in distance between first gill slits, 1.14 (1.19–1.24) in distance between fifth gill slits. Upper jaw arched slightly, not indented at symphysis; lower jaw not angular, not double convex; lateral teeth partly concealed by lobe of nasal curtain. Teeth of female holotype unicuspid with slightly raised rhomboidal cusps in middle of jaws; arranged in obvious longitudinal rows; main cusps short, tips blunt to narrowly rounded, posteriorly directed in upper jaw and best developed near symphysis; cusps on lateral teeth shorter, broader or absent.

Pelvic fins moderately forked; anterior lobe relatively short, broad, lateral margin entire, distal and inner margins incised; posterior lobe very elongate 15.9% (16.3–18.0%) TL, lateral margins serrate, weakly convex, free rear tip narrowly rounded to somewhat angular; inner margin almost straight; anterior lobe 0.80 (0.75–0.83) times posterior lobe. Clasper unknown. Tail slender, depressed; relatively broad at base, tapering strongly from its base to tail tip; not expanded at its midlength; width at insertions of pelvic fins 2.01 (1.78–2.16) times width at midlength of tail and 2.97 (2.19–2.82) times width at first dorsal-fin origin respectively; length from rear of cloaca 0.90 (0.75–0.92) times distance from tip of snout to rear of cloaca; anterior cross-section broadly suboval, not more convex on dorsal surface than ventral surface; almost flat ventrally near tail apex; width 1.66 (1.61–1.91) times

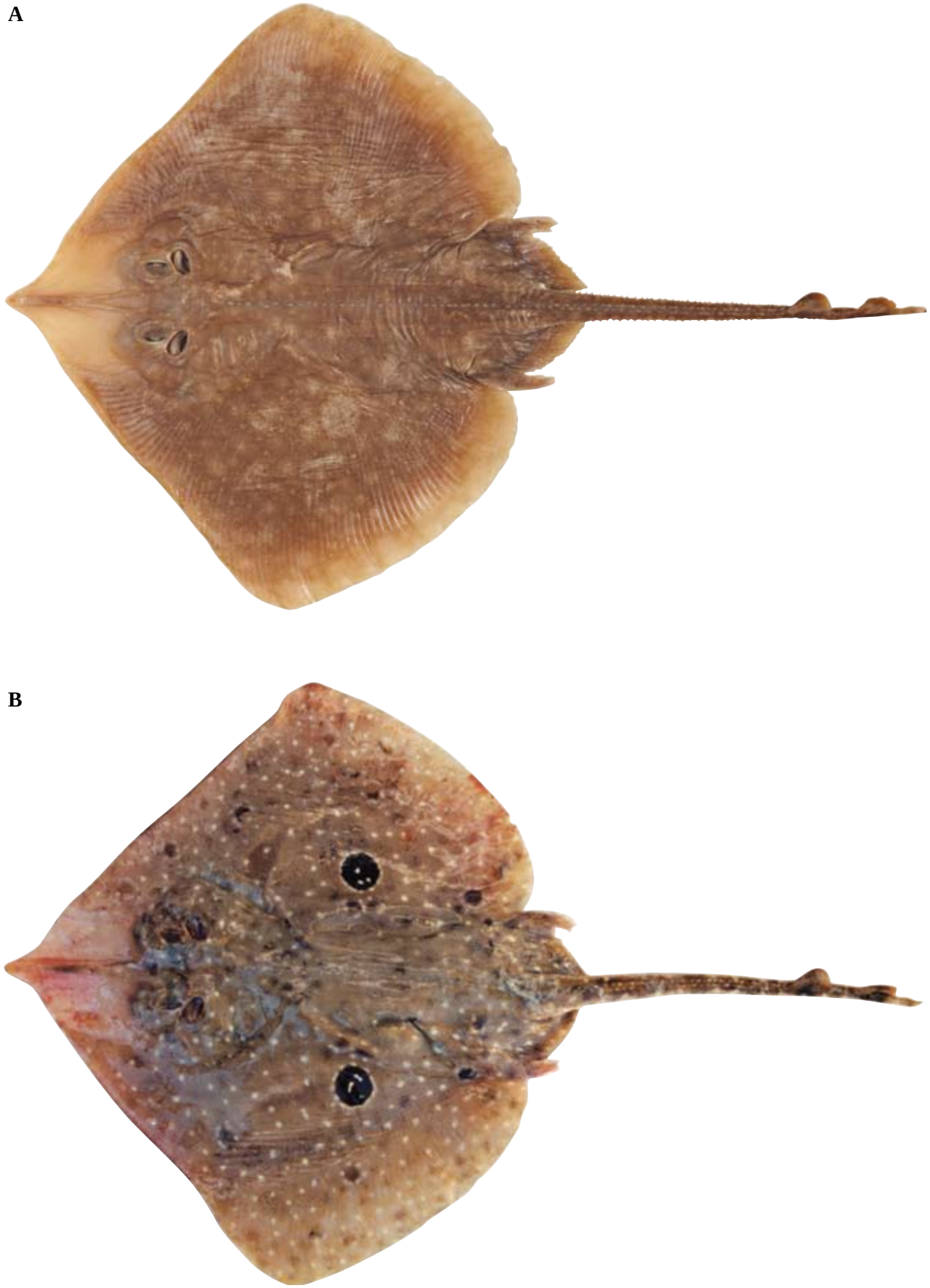

Figure 1. Dorsal surface of *Okamejei jensenae* sp. nov., female holotype (PNM 15096, 488 mm TL): A. preserved; B. fresh.

Table 1. Morphometrics for the female holotype of *Okamejei jensenae* sp. nov. (PNM 15096) and ranges and means for the 4 measured specimens. Values are expressed as percentages of total length (TL).

		n = 4		
	Holotype	Min.	Max.	Mean
Total length (mm)	488	464	533	
Disc width	65.9	64.7	70.6	67.4
Disc length (dir)	57.1	56.1	61.1	58.1
Snout to maximum width	31.8	30.7	33.6	31.9
Snout length (preorbital) - dir	16.1	15.6	17.2	16.5
Snout to spiracle	21.3	20.5	22.6	21.8
Head - dorsal	22.4	21.8	24.4	23.2
Orbit diameter	3.4	3.5	3.9	3.7
Orbit and spiracle length	5.1	5.2	5.9	5.5
Spiracle length - main pore	2.8	2.4	2.9	2.6
Distance between orbits	4.8	4.6	5.1	4.9
Distance between spiracles	5.9	5.9	6.5	6.2
Distance-snout to cloaca	52.7	52.1	56.2	53.6
Cloaca to D1	31.5	27.1	30.3	29.0
Cloaca to D2	38.5	35.5	39.2	37.2
Cloaca to caudal origin	43.5	40.8	44.2	42.2
Distance-cloaca to caudal fin tip	47.3	43.8	47.9	46.2
Snout length (pre upper jaw)	17.0	16.5	18.1	17.3
Prenasal length	13.7	13.1	14.4	13.8
Head length to fifth gill	30.6	30.2	32.3	31.3
Mouth width	8.8	8.3	10.0	9.0
Distance between nostrils	8.1	7.7	8.5	8.1
Nasal curtain-length	4.9	4.8	5.7	5.2
Nasal curtain-total width	10.3	10.4	10.5	10.4
Nasal curtain - min width	6.0	5.7	6.2	5.9
Nasal curtain - lobe width	2.1	2.2	2.6	2.3
Width of 1st gill opening	1.9	1.7	2.0	1.8
Width of 5th gill opening	1.1	1.1	1.4	1.3
Distance between 1st gill openings	16.7	16.7	17.4	17.0
Distance between 5th gill openings	9.3	9.5	10.1	9.8
Length of anterior pelvic lobe	12.8	12.6	14.5	13.4
Length of posterior pelvic lobe	15.9	16.3	18.0	17.1
Pelvic base - width	10.9	11.1	11.8	11.5
Tail at axil pelvic fins - width	4.4	3.5	4.7	3.9
Tail at axil pelvic fins - height	2.6	2.0	2.5	2.2
Tail at midlength - width	2.2	1.9	2.2	2.0
Tail at midlength - height	1.3	1.1	1.3	1.2
Tail at D1 origin - width	1.5	1.6	1.7	1.6
Tail at D1 origin - height	1.0	1.0	1.0	1.0
D1 base - length	4.9	4.9	5.6	5.2
D1 - height	2.5	1.8	2.2	2.0
D1 orig to caudal fin tip	15.8	15.6	18.6	17.2
D2 orig to caudal fin tip	8.8	8.4	9.8	9.0
Caudal-fin length	3.8	2.4	5.1	3.7
Interdorsal space	1.7	3.1	5.0	3.8

Figure 2. Ventral surface of *Okamejei jensenae* sp. nov., female holotype (PNM 15096, 488 mm TL, preserved).

height at insertion of pelvic fin, 1.73 (1.63–1.79) times height at midlength, 1.45 (1.59–1.65) times height at first dorsal fin origin; lateral tail fold moderately well developed, narrow but obvious for most of its length, its origin near tip of pelvic fin; fold obscure at tail tip. Dorsal fins of similar shape and size (first dorsal fin not taller and not more upright than second); first dorsal-fin height 1.95 (2.46–2.63) in base length; fins low, rounded, strongly raked, elongate with long bases; anterior margins convex, apices broadly rounded, posterior margins short and convex, inner margins short (often longer on second dorsal); interdorsal distance very long, 2.35 (1.20–2.28) in length of first dorsal-fin base; distance from first dorsal-fin origin to tail tip 3.23 (3.09–3.63) times dorsal-fin base length, 4.18 (3.37–6.39) times caudal-fin length; first dorsal-fin base 1.30 (1.01–2.07) times caudal-fin length. Epichordal caudal-fin lobe long-based, low, its height subequal to half tail width at its origin; pointed or truncate distally, its posterodorsal margin usually straight, often irregular; connected to second dorsal fin by low ridge; hypochordal caudal lobe vestigial.

Dorsal surface of female holotype with small (but prominent) orbital, nuchal, mid-dorsal and tail thorns. Orbital thorns of holotype small, pungent, variable in size, continuous around orbit and extending to spiracle; forming an incomplete rosette; about 10–12 (4 on preorbit, 2–5 on midorbit, 3–4 on postorbit), paratypes similar, often less well developed along mid orbit; upright, recurved posteriorly. Nuchal thorns small, semi erect, similar in size, continuous along midline of disc in a single series and merging with tail series; about 30 thorns forward of posterior cloaca, commencing immediately posterior of head, interspacing mostly regular with a few gaps. Malar and alar thorn morphology unknown. Tail thorns in 3 closely spaced rows on midline and mainly 2 well-developed lateral rows on each side; dorsolateral rows absent; central median row consisting of about 23 thorns, continuous with series along mid-disc, progressing to first dorsal fin, closely flanked either side by dense rows of about 31–35 latero-medial thorns; most thorns of latero-medial rows larger (about twice height) of those in central median row; about 7 small interdorsal thorns. Lateral tail rows dense, situated close to lateral folds, commencing above pelvic-fin insertions; thorns in ventralmost series semi-erect, only slightly larger than central median thorns, about 40 before first dorsal fin; thorns in uppermost rows much smaller than those below. Thorn rows of tail in paratypes of very similar configuration to holotype.

Denticles present on both surfaces, confined mainly to head and anterior margin of disc. On dorsal surface, patches of granular denticles present above rostral and

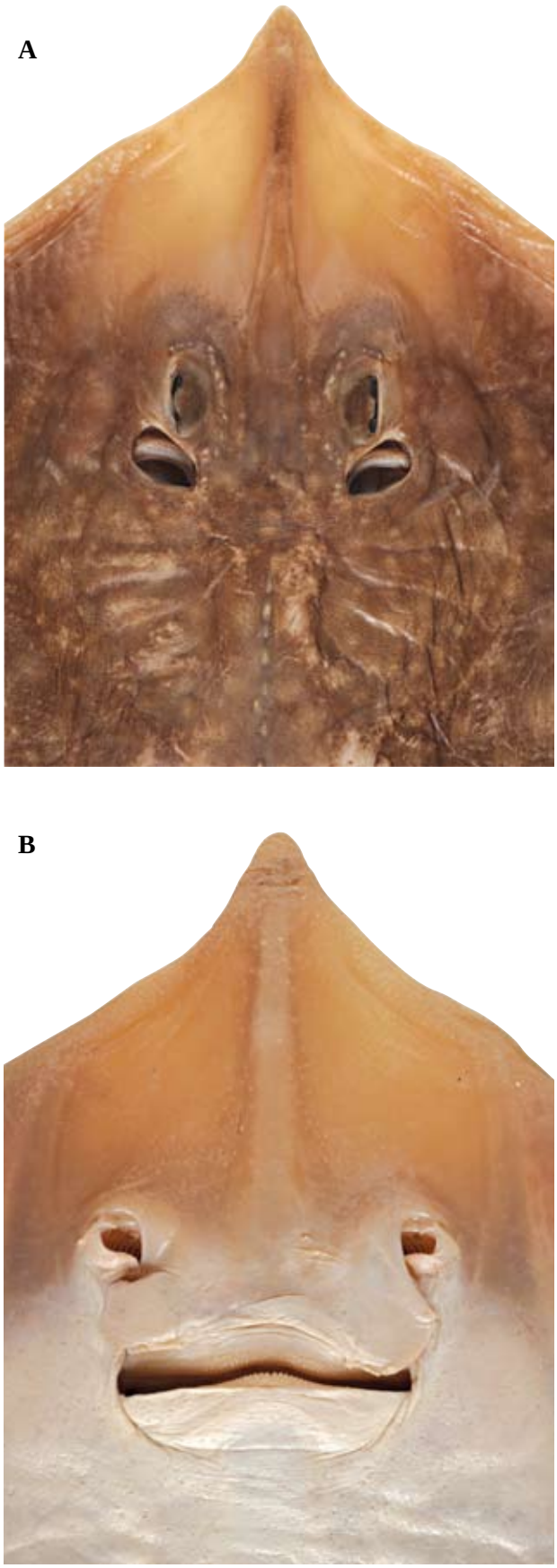

Figure 3. *Okamejei jensenae* sp. nov., female holotype (PNM 15096, 488 mm TL, preserved): A. dorsal head; B. ventral head.

orbital cartilages, and above propterygium; denticles on anterior lateral disc densest beside orbito-spiracular region, not confined to disc margin and largely absent between snout apex and tip of propterygium; some paratypes with denser coverage over snout, but prominent band of denticles near edge of disc beside orbito-spiracular region consistently present. On ventral surface, variable patches of granular denticles confined to preoral snout and along disc margin to level of mouth, internasal flap mostly naked.

Meristics (n=4): Tooth rows in upper jaw 70 in female holotype (61–76 in 3 female paratypes); lower jaw 67 (70–75). Pectoral-fin propterygial radials 33–34 (32–35); mesopterygial radials 15–16 (14–18); metapterygial radials 32–33 (31–34); total radials 81–82 (80–82). Pelvic-fin radials in females 1 (1) + 20 (20–22). Trunk centra 29 (26–31); predorsal caudal centra 56 (50–53); predorsal centra 85 (79–84); centra between origins of dorsal fins 15 (16–18); diplospondylous centra 107 (106–107); total centra about 136 (133–138).

COLORATION.— In holotype, when fresh: Dorsal surface of disc, pelvic fins and tail brownish; densely covered with slightly darker brownish blotches and white spots, with a pair of large dark pectoral markings; membrane beside rostral cartilage pale to translucent, demarcated from rest of head; brownish blotches slightly smaller than spiracular opening; white spots diffuse edged, densely and more or less evenly spaced, less than a third diameter of brownish blotches. Pectoral markings large, circular, diameter only slightly smaller than length of orbito-spiracular region; blackish centrally with additional embedded white flecks and a white spotted margin; marking highly deciduous, absent or reduced to a whitish marking in three of four types after preservation (see Fig. 1a); orbital membrane dark brown, iris blackish; dorsal fins brownish anteriorly, paler posteriorly, each with a dark saddle below their bases; caudal fin paler than dorsal fins. Ventral surface of disc and pelvic fins mainly white; broad, semi-translucent yellowish margin extending forward from pectoral-fin insertion, around disc and onto snout; nasal region whitish, strongly demarcated from anterior snout adjacent; sensory pores minute, greyish, barely detectable; tail whitish, usually with yellowish brown longitudinal stripes along its margins. In preservative: Differs markedly from fresh state on dorsal surface; pectoral marking usually removed, evident as a whitish patch; white spots also usually removed, brownish blotches persistent but paler than main colour of disc; ventral coloration similar to fresh state.

SIZE.— To at least 533 mm TL; all type specimens are females, so details of maturity in males unknown.

DISTRIBUTION.— Off eastern Borneo and the Philippines in the Sulu Sea in 110–118 m. Depth range (110–118 m) based on information for a single paratype (IPPS 2010–03) so it is not well defined; however, probably

mainly on the mid-continental shelf rather than inshore.

ETYMOLOGY.— The epithet honours the contribution made to shark and ray taxonomy by cestode parasitologist, Dr Kirsten Jensen. During an extensive field survey of fish markets of Borneo, conducted over the past decade, Dr Jensen captured digital images of all chondrichthyan specimens sampled and provided images of most species for a field guide to the sharks and rays of Borneo (Last *et al*., in press). Along with a close colleague, Dr Janine Caira, she has gained a broad knowledge of the taxonomy of the chondrichthyan fauna, as well as their invertebrate parasites. Proposed vernacular name: 'Sulu Sea Skate'.

REMARKS.— *Okamejei jensenae* has a unique colour pattern with a very large, dark pectoral marking with a whitish border and inner spotting. Within the genus, this character is shared by *Raja fusca* Garman, 1885 (*sensu* Ishiyama, 1967) from the western North Pacific which is considered to be a junior synonym of *Okamejei kenojei* (Müller & Henle, 1841) (Ishihara, 1987; Eschmeyer, 2010), and *O. powelli* (Alcock, 1898) from India and Myanmar. Ishiyama's figure of *R. fusca* resembles *O. jensenae* in general appearance, but has more evenly distributed tail thorn rows and is covered in dark spots. Also, according to Ishiyama's description, *R. fusca* has separate median denticle patches in the nuchal region and on the posterior disc (rather than a single series along entire disc). Ishihara (1987) gives upper-jaw tooth row counts of 43–55 for *O. kenojei* (vs. 61–76 in *O. jensenae*) and predorsal caudal centra 35–46 (vs. 50–56). *Okamejei jensenae* does not closely resemble any other species of *Okamejei* from the western North Pacific. The ocellated Indian Ocean skate *Okamejei powelli* is not well defined. However, according to Fowler (1941), based mainly on Alcock (1899), this species does not have a continuous series of thorns along the median disc, the eye is 5.2–6.3 (vs. 4.0–5.0) in the snout length, and it has 55 rows of teeth in both jaws (vs. 61–76).

Figure 4. Orbito-spiracular region of *Okamejei jensenae* sp. nov., female paratype (IPPS 2010–03, 496 mm TL, preserved), showing the relative sizes and positions of the spiracle and orbit and their associated thorns.

Figure 5. Ventral view of the oronasal region of *Okamejei jensenae* sp. nov., female paratype (IPPS 2010–03, 496 mm TL, preserved).

Dipturus kwangtungensis (Chu, 1960)

Figs 7–10; Table 2

Material examined. 3 specimens: CSIRO H 7100–01, immature male 411 mm TL, west of Miri, Sarawak, Malaysia, South China Sea, 04°57.40′ N, 113°04.60′ E, 99–108 m, 13 Aug. 2005; IPPS 2010–01, female 446 mm TL, IPPS 2010–02, west of Miri, Sarawak, Malaysia, South China Sea, 04°57.40′ N, 113°04.60′ E, 99–108 m, 13 Aug. 2005.
Other material (not examined, based on Ishihara, 1987). 3 specimens: SFI 57–0676 (possible holotype), immature male 336 mm TL, South China Sea; SFI 57–0675 (paratype) immature male 405 mm TL, SFI 57–0674 (paratype) female 499 mm TL, South China Sea.

DIAGNOSIS.— A medium-sized species of *Dipturus* (to at least 50 cm TL) with the following combination of characters: disc with bluntly angular apices, but not especially broad, width 67–70% TL, about 1.2 times its length; snout angle acute 79–80°; tail not elongate, length 0.8–0.9 in distance from snout tip to rear of cloaca; tail slender, width 1.2–1.4 times height at its midlength, 1.3–1.6 times at first dorsal-fin origin; pre-upper jaw length 18–21% TL, 2.2–2.4 times internasal width; ventral head length 33–35% TL; snout length about 4.1 times interorbital width; orbit diameter about 93% interorbital width in male, about 76% in female; first dorsal-fin height 1.6–2.1 in its base length; distance from first dorsal-fin origin to tail tip 3.7–4.5 times first dorsal-fin base length, 3.0–3.4 times caudal-fin length; pelvic fins of medium size, length of posterior lobe 15–16% TL, length of anterior lobe 87–98% of posterior lobe; adult clasper unknown; anterior margins of dorsal surface without denticle bands; nuchal thorns absent; tail thorns well developed, in single staggered median row in both sexes; total pectoral radials 82; trunk centra 30–31; predorsal centra 73–79; total centra about 135–141; tooth rows in upper

Figure 6. Profile of the tail of the female holotype (PNM 15096, 488 mm TL, preserved) of *Okamejei jensenae* sp. nov.: A. dorsal view; B. lateral view; C. lateral view of procaudal region.

jaw 34–36; entire dorsal surface coarsely mottled, dark brown and yellowish to greyish white, lacking ocellate markings; most of ventral surface uniformly dark greyish brown; rostral cartilage weakly demarcated from rest of snout dorsally, better defined ventrally; ventral sensory pores well defined on snout, unobvious elsewhere, not surrounded by greyish blotches; dorsal fins without dark saddles, caudal fin with 1 or 2 dark bars.

DESCRIPTION.— Disc weakly quadrangular, 1.19 times as broad as long in 446 mm TL female IPPS 2010–01 (1.18 times in 411 mm TL immature male CSIRO H 7100–01); angle in front of orbits acute, 79° (80°); axis of greatest width 64% (63%) of disc length; anterior margin double concave, concave anteriorly toward snout apex, convex beside and slightly forward of eyes, concave beside spiracles; pectoral-fin apex bluntly angular; posterior margin weakly convex; free rear tip very broadly rounded. Head moderately large, preorbital snout length 5.34 (4.43) times orbit length, 4.08 (4.10) times interorbit; pre-upper jaw length 2.36 (2.18) times internarial distance. Snout tip very well produced, prominent, narrowly pointed, similar in juvenile male and female; no fleshy process at apex. Orbit diameter 0.76 (0.93) times interorbital width. Spiracle small, length 1.61 (1.61) in orbit diameter; opening teardrop-shaped. Nostril broadly suboval, distorted; anterior nasal flap expanded slightly, its lateral margin weakly tubular, its anterior margin weakly lobe-like and mostly concealed beneath nasal curtain, its posterior inner margin barely concealed by nasal curtain. Nasal curtain skirt shaped, lateral margins subparallel, not produced posterolaterally, posterior distal margin with long fringe; internarial distance 1.79 (1.86) in distance between first gill slits, 0.98 (1.01) in distance between fifth gill slits. Upper jaw arched in both sexes, not indented at symphysis; lower jaw not angular, not double convex; lateral teeth mostly concealed by lobe of nasal curtain. Teeth in quincunx, with broad oval crowns and short cusps, similar in female and immature male.

Pelvic fin very deeply forked; anterior lobe long, slender, its lateral margin entire, distal and inner margins incised; posterior lobe not greatly extended, 15.7% (14.5%) TL, its lateral margin finely serrate, free rear tip angular, inner margin straight; anterior lobe 0.87 (0.98) times posterior lobe. Clasper of adult male unknown. Tail very slender, depressed slightly; relatively narrow at base, tapering gradually posteriorly, tapering rapidly to tail tip beyond second dorsal fin; not expanded at its midlength; width at insertions of pelvic fins 2.11 (2.67) times width at midlength of tail and 2.03 (2.73) times width at first dorsal-fin origin respectively; length from rear of cloaca 0.79 (0.88) times distance from tip of snout to rear of cloaca; anterior cross-section suboval, more convex on dorsal surface than ventral surface, surfaces equally

Figure 7. *Dipturus kwangtungensis*, female (IPPS 2010–01, 446 mm TL, preserved): A. dorsal surface; B. ventral surface.

Table 2. Morphometrics for the presumed female holotype of *Dipturus kwangtungensis* (SFI 57-0676), and ranges for 2 paratypes (from Ishihara, 1987) and 2 Borneo specimens. Ranges for 5 specimens of *D.* cf. *kwangtungensis* var A and measurements for one specimen of *D.* cf. *kwangtungensis* var B are also extracted from Ishihara (1987). Values are expressed as percentages of total length (TL).

	D. kwangtungensis					*D.* cf. *kwangtungensis*		
	Holotype?	Paratypes (n=2)		Borneo material (n=2)		var A (n = 5)		var B
		Min.	Max.	Min.	Max.	Min.	Max.	
Total length (mm)	336	405	499	411	446	485	757	516
Disc width	67.9	66.5	69.9	66.8	70.0	67.0	72.6	64.0
Disc length (dir)	57.0	54.0	55.4	56.5	59.0	57.3	59.9	54.9
Snout to maximum width	37.5	35.4	37.0	35.8	37.8	31.2	36.3	33.8
Snout length (preorbital) - dir	19.2	17.9	20.4	17.6	19.6	14.8	16.2	13.9
Snout to spiracle	–	–	–	23.2	25.3	–	–	–
Head - dorsal	25.9	24.7	26.1	24.6	27.0	22.5	23.0	21.5
Orbit diameter	2.6	2.5	2.8	3.7	4.0	3.2	4.2	3.8
Orbit and spiracle length	–			5.7	5.7	5.3	6.2	6.1
Spiracle length - main pore	–	–	–	2.3	2.5	–	–	–
Distance between orbits	4.8	4.6	4.8	4.3	4.8	4.8	5.7	4.6
Distance between spiracles	7.1	6.8	6.8	6.2	6.2	6.7	8.0	6.3
Distance-snout to cloaca	54.3	52.6	53.4	53.1	55.9	53.6	55.6	53.0
Cloaca to D1	–	–	–	28.4	28.9	–	–	–
Cloaca to D2	–	–	–	35.0	35.3	–	–	–
Cloaca to caudal origin	–	–	–	39.5	41.0	–	–	–
Distance-cloaca to caudal fin tip	45.7	46.6	47.4	44.1	46.9	44.8	46.4	47.0
Snout length (pre upper jaw)	19.5	18.4	20.2	18.3	21.3	14.8	16.3	13.6
Prenasal length	16.2	14.9	16.7	15.6	17.4	11.8	12.6	11.1
Head length to fifth gill	34.2	34.3	35.1	32.8	35.2	30.2	31.5	30.0
Mouth width	9.8	9.1	9.3	8.9	9.2	8.9	9.6	8.4
Distance between nostrils	8.8	8.8	9.1	8.4	9.0	8.1	8.6	7.6
Nasal curtain-length	3.7	3.8	4.2	4.8	5.4	4.9	5.8	5.0
Nasal curtain-total width	–	–	–	9.5	9.7	–	–	–
Nasal curtain - min width	–	–	–	6.5	6.6	–	–	–
Nasal curtain - lobe width	–	–	–	1.7	1.9	–	–	–
Width of 1st gill opening	–	–	–	1.7	1.8	–	–	–
Width of 5th gill opening	–	–	–	1.1	1.2	–	–	–
Distance between 1st gill openings	–	–	–	15.6	16.1	–	–	–
Distance between 5th gill openings	–	–	–	8.5	8.8	–	–	–
Clasper-postcloacal length	–	–	–	7.9	7.9	–	–	–
Length of anterior pelvic lobe	13.7	12.7	12.7	13.6	14.2	9.5	12.3	10.4
Length of posterior pelvic lobe	–	–	–	14.5	15.7	13.1	17.7	15.2
Pelvic base - width	–	–	–	7.6	8.2	–	–	–
Tail at axil pelvic fins - width	–	–	–	3.2	3.4	–	–	–
Tail at axil pelvic fins - height	–	–	–	1.9	2.1	–	–	–
Tail at midlength - width	–	–	–	1.3	1.5	–	–	–
Tail at midlength - height	–	–	–	1.0	1.1	–	–	–
Tail at D1 origin - width	–	–	–	1.3	1.6	–	–	–
Tail at D1 origin - height	–	–	–	1.0	1.0	–	–	–
D1 base - length	4.5	3.4	4.8	3.8	4.3	4.0	4.7	4.6
D1 - height	2.4	1.8	2.6	2.1	2.4	2.2	3.4	2.1
D1 orig to caudal fin tip	15.7	15.4	18.9	15.8	16.9	14.7	17.0	18.7
D2 orig to caudal fin tip	–	–	–	9.1	10.5	–	–	–
Caudal-fin length	–	–	–	4.6	5.7	–	–	–
Interdorsal space	2.5	3.4	4.0	2.5	2.7	2.3	3.4	4.1

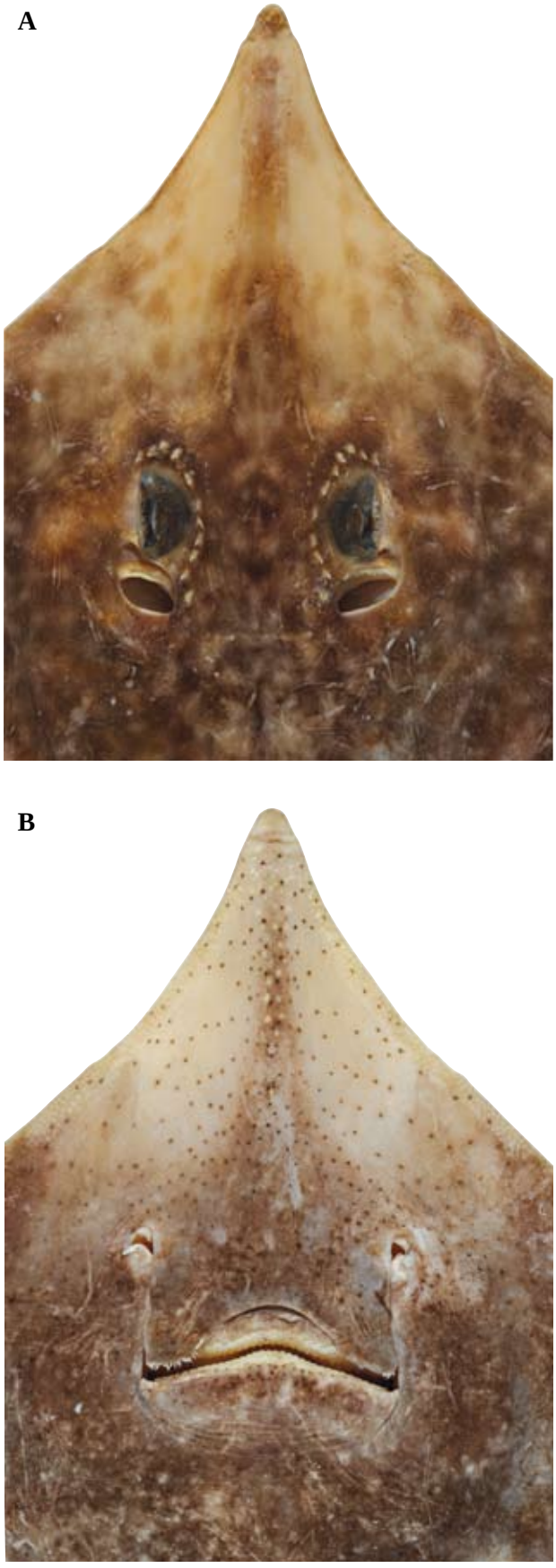

Figure 8. *Dipturus kwangtungensis*, immature male (CSIRO H 7100–01, 411 mm TL, preserved): A. dorsal head; B. ventral head.

convex at tail midlength, weakly convex ventrally near tail apex; width 1.69 (1.61) times height at insertion of pelvic fin, 1.43 (1.23) times height at midlength, 1.63 (1.32) times height at first dorsal fin origin; lateral tail fold very weak, originating about an eye diameter behind pelvic-fin tip and continuing as a fleshy ridge to beneath dorsal fins, width below dorsal fins <1 mm. Dorsal fins small, of similar shape and size (first dorsal fin not taller and not more upright than second); first dorsal-fin height 2.07 (1.59) in base length; both fins very low and strongly raked, elongate with short bases; their anterior margins weakly convex, apices rounded, posterior margins very short and convex, inner margins relatively long; interdorsal distance short, 1.81 (1.44) in length of first dorsal-fin base; distance from first dorsal-fin origin to tail tip 3.70 (4.46) times dorsal-fin base length, 3.41 (2.95) times caudal-fin length; first dorsal-fin base 0.92 (0.66) times caudal-fin length. Epichordal caudal-fin lobe small, low, its height less than tail width at its origin; pointed distally, its posterodorsal margin usually weakly convex; connected to second dorsal fin by low ridge; hypochordal caudal lobe barely detectable.

Dorsal surface with well-developed orbital and tail thorns; nuchal thorns absent; alar and malar thorn morphology and distribution unknown; thorns in continuous rosette around orbit 9–11 (4 on preorbit, 3–5 on midorbit, 2 on postorbit); of moderate size, strong, semi-erect, usually recurved posteriorly. Tail thorns about 17–21 predorsally, in a single staggered series along midline commencing over pelvic-fin insertion or inner margin; larger than around eye (almost twice their length on average); very pungent, with long, narrow bases; interdorsal thorns 1–2. Denticles poorly developed, absent from entire dorsal surface (apart from extreme snout tip) in material examined; ventral surface mostly naked, large granular denticles densely arranged in a band along anterior margin, almost reaching level of nostrils, and slightly larger, more widely spaced denticles along rostral cartilage;

Meristics (new material n=2 given first; type data when available based on Ishihara, 1987, in parentheses): Tooth rows in upper jaw 34–36 (34–35 in types); lower jaw 34–35. Pectoral-fin propterygial radials 30–32; mesopterygial radials 15–16; metapterygial radials 35–38; total radials 82. Pelvic-fin radials in female 1 + 22; in male 1 + 21. Trunk centra 30 (30–31); predorsal caudal centra 47–49 (43–48); predorsal centra 77–79 (73–79); centra between origins of dorsal fins 14–15; diplospondylous centra about 105–111; total centra about 135–141.

COLORATION.— In preservative: Dorsal surface of disc, pelvic fins and tail densely mottled, covered with a pattern of yellowish white and dark blotches; slightly paler and more uniform yellowish areas beside rostral cartilage; tips of anterior pelvic-fin lobe white; orbital membrane dark brown, iris black; dorsal and caudal fins uniformly dark brownish to black. Ventral surface of disc and tail almost uniformly dark brown; whitish beside

rostral cartilage, around cloaca, on claspers, and at tips of anterior pelvic-fin lobes; some whitish scrapes and scars are likely artefacts; sensory pores well developed on head, less obvious near gills; pores small, brownish black, not surrounded by greyish blotches.

SIZE.— To at least 499 mm TL, almost certainly much larger; male maturity size unknown but claspers undeveloped at 411 mm TL.

DISTRIBUTION.— Types collected from the East China Sea, off China; current literature identifications of this species should be treated with caution. Two newly collected specimens from the South China Sea, off western Borneo, constitute the most southerly confirmed limits of its range.

REMARKS.— There are inconsistencies in the literature regarding holotype details and the sizes of paratypes of *Dipturus kwangtungensis*, which we unfortunately were unable to confirm by either accessing Chu's (1960) original description or examining his types. Ishiyama (1967), based on a Chinese-English translation from Chu's (1962) redescription of the species (misspelt as *Raja kwantungensis*), claimed that the primary type is a female (439 mm TL), and the other types are smaller (330 and 400 mm TL respectively). Ishihara (1987), also followed by Eschmeyer (2010), listed the holotype as SFI 57–0676; according to Ishihara, this specimen is an immature male, 336 mm TL (presumably the smallest paratype of Ishiyama). However, the specimen considered by Ishiyama to be the holotype, and presumably the specimen selected by Chu, must be SFI 57–0674, a female, 499 mm TL (Ishiyama's 439 mm TL is presumably a typographic error as the morphometrics given by Ishihara are consistent with other specimens). Hence, the determination of the actual designated holotype needs further investigation.

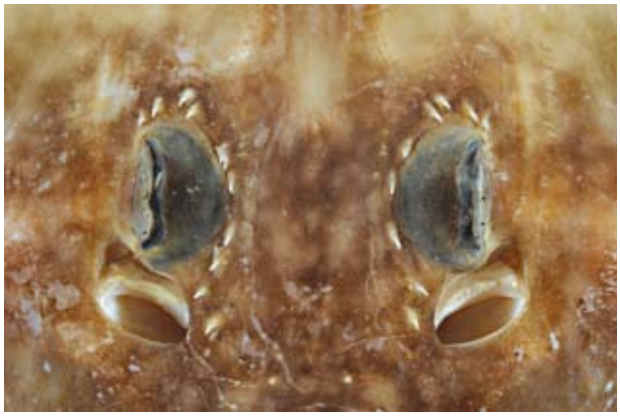

Figure 9. Orbito-spiracular region of *Dipturus kwangtungensis*, female (IPPS 2010–01, 446 mm TL, preserved), showing the relative sizes and positions of the spiracle and orbit and their associated thorns.

Figure 10. Ventral view of the oronasal region of *Dipturus kwangtungensis*, female (IPPS 2010–01, 446 mm TL, preserved).

Ishihara (1987), when revising the taxonomy of western North Pacific species of the genus *Raja* (now including former subgenera genera *Dipturus* and *Okamejei*), regarded *Raja kenojei* sensu Ishiyama (1958, 1967) as being non-conspecific with *Raja kenojei* Muller & Henle, 1841. However, rather than describing Ishiyama's skate as a new species, Ishihara instead chose to use *Raja* (now *Dipturus*) *kwangtungensis* Chu, 1960 for this species rather than adding to the considerable taxonomic confusion already existing in the taxonomy of western North Pacific species of the genus *Raja*. Moreover, it is important to be aware that the zoogeography of the genus *Raja* at the periphery of the western North Pacific, particularly of *Okamejei* and *Dipturus*, had not been clarified at that time.

The first Borneo specimens of *Dipturus kwangtungensis* conform closely to Ishihara's data for the three types (see Table 1, Ishihara, 1987), and the images of SFI 57–0676 (Figs 1A, B, Ishihara, 1987) closely resemble our material in appearance. However, the series of 9 specimens selected and measured by Ishihara do not appear to be conspecific; as many as three species may be represented in this series. The inclusion of suspected multiple taxa in his redescription has possibly caused confusion over the identity of this species. The three types and six other morphometric specimens (MTUF 25047, MTUF 25048, MTUF 25072, MTUF 35014, MTUF 35066 and MTUF 94973), typically from Japanese seas, were compared to our material (see Table 2). These specimens differ from Chu's types and our material in several characters: snout to max width 0.54–0.61, n=6 (vs. 0.63–0.69 in types and our material, n=5) of disc length; snout length 3.7–4.4 (vs. 2.8–3.2) times interorbital distance; pre-upper jaw 2.0–2.4 (vs. 1.8–1.9) times internasal width; snout length 0.37–0.44 (vs. 0.29–0.36) of post-cloacal tail length; and pelvic anterior lobe length 0.87–0.98 (vs. 0.68–0.81) of its posterior lobe length. Allometric differences do not appear to be involved.

Figure 11. Profile of the tail of the female (IPPS 2010–01, 446 mm TL, preserved) of *Dipturus kwangtungensis*: A. dorsal view; B. lateral view; C. lateral view of procaudal region.

In addition, specimen MTUF 94973 (Ishihara, 1987; Fig 1C) is sexually mature at 52 cm TL, whereas other male specimens from Japan are mature at 72 cm TL (MTUF 35014) and still immature at 53 cm TL (MTUF 25047). The snout length of MTUF 94973 (13.9% TL) is considerably smaller than typical *D. kwangtungensis* (17.6–20.4% TL), and noticeably smaller than the other Japanese specimens (14.8–15.3% TL) of similar size. Other morphometric differences exist between these groups of specimens that are atypically large for *Dipturus* skates of the same species (see for example Last, 2008). The Japanese material needs to be re-examined in the light of these observations to determine their identity, and in particular resolve forms currently identified as *O. kenojei* and *D. kwangtungensis* (Ishihara pers. comm.).

Comparative material (not examined, based on Ishihara, 1987).

Dipturus cf. *kwangtungensis* var A: HUMZ 35014, mature male 721 mm TL, Japan; HUMZ 35066, female 757 mm TL, Japan; MTUF 25047, immature male 527 mm TL, Japan; MTUF 25048, female 502 mm TL, Japan; MTUF 25072, immature male 485 mm TL, Japan.

Dipturus cf. *kwangtungensis* var B: HUMZ 94973, mature male 516 mm TL, East China Sea.

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Description of a new stingray, *Pastinachus gracilicaudus* sp. nov. (Elasmobranchii: Myliobatiformes), based on material from the Indo–Malay Archipelago

Peter R. Last[1] & B. Mabel Manjaji-Matsumoto[2]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] School of Zoology, Borneo Marine Research Institute, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, MALAYSIA

ABSTRACT.— The Indo–Malay Archipelago, which has the richest dasyatid fauna of any region, is also a diversity hotspot for the genus *Pastinachus*. A new cowtail stingray is described based on material collected off Malaysian and Indonesian Borneo, and Singapore. The new species is unique within the genus in being of medium size (ca 75 cm DW) and having a broad disc, an obtuse snout, 2–3 large mid-scapular pearl thorns, a low ventral skin fold that is usually pale, and no enlarged denticles on its snout tip. It also differs from *P. sephen* and two other *Pastinachus* species occurring off Borneo in the structure of the COI gene.

Key words: *Pastinachus gracilicaudus* –new species – stingray – Dasyatidae – Indo–Malay Archipelago

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

Until recently, the stingray genus *Pastinachus* Rüppell was considered to be a monotypic genus represented by a single widespread species, *P. sephen* (Forsskål, 1775). Forms of *Pastinachus* occur across the Indo–Pacific from the Red Sea to Australia, including Melanesia, Micronesia, and the China Seas (Last & Compagno, 1999). Two other supraspecific taxa, *Hypolophus* Müller & Henle, 1837 and *Makararaja* Roberts, 2007, are similar and may both be junior synonyms of *Pastinachus*.

The group is presently being reviewed by one of us (PL) and these studies have shown that several forms previously identified as *P. sephen* belong to other valid species. A new species, *Pastinachus solocirostris* Last, Manjaji & Yearsley, was described recently from Malaysian Borneo and Indonesia (Last *et al*., 2005), and an Australasian species, *P.* (as *Taeniura*) *atrus* (Macleay, 1883), type locality Port Moresby (New Guinea), appears to be valid (Last & Stevens, 2009).

Another four nominal species are presumed to be junior synonyms of *P. sephen*: *Raia fluviatilis* Hamilton, 1822 (Roberts, 1998), *Trigon forskalii* Rüppell, 1829 (Nishida & Nakaya, 1990), *Dasybatus gruveli* Chabanaud, 1923 (Last & Compagno, 1999), and *Raia sancur* Hamilton, 1822 (Talwar & Jhingran, 1991). These taxa conform to either *P. sephen* or *P. atrus*. However, another *Pastinachus*, a relatively small species from the Indo–Malay Archipelago, has been confused with members of the *sephen* complex. This species, first identified during the Darwin Foundation survey of the elasmobranchs of Sabah, has an unusually low, pale ventral cutaneous fold on the tail and matures at a much smaller size than either *P. sephen* or *P. atrus*.

METHODS

Features of the disc (including squamation, tooth row counts and meristics) closely follow standards adopted by Compagno & Roberts (1982), Manjaji (2004), Last *et al*. (2005), Manjaji-Matsumoto & Last (2006), and Last *et al*. (2006). Morphometric methods generally follow Compagno & Heemstra (1984) and meristic data were obtained from radiographs following Compagno & Roberts (1982) and Last & White (2008). Additional morphometric characters used by Last *et al*. (2005) to account for other diagnostic features, such as the shape of the tail and its associated ventral skin fold, are important in distinguishing different species of the genus *Pastinachus*. These included tail widths and depths (height), which were recorded at the origin and insertion of the skin fold as well as at quartile intervals between, along with the depth (height) of the fold at each of these points. A total of 54 measurements, expressed as proportions of disc width (DW, see Table 1), were taken for the holotype (SMEC 35) and 19 paratypes (165–717 mm DW), including 5 late-stage embryos or neonates

(165–266 mm DW); data for some of these specimens were incomplete due to damage or prior removal of structures. Data for embryos are included separately in Table 1, but not included in the diagnosis or description.

Radiographs were taken and counts obtained by John Pogonoski in his capacity as manager of the Australian National Fish Collection Skeletal Image Collection. Meristic details were obtained for 6 paratypes (CSIRO H 5480–03, CSIRO H 5615–03, CSIRO H 5864–03, CSIRO H 5864–04, CSIRO H 7109–01 and SFRI 27404.2); the holotype remained in Sabah during this study and was unable to be radiographed.

Barcode of Life (BOLD, www.barcodinglife.org) protocols follow Ward *et al*. (2005) and mitochondrial cytochrome c oxidase I (COI) gene sequences were obtained and aligned using ClustalX software and analysed in MEGA 4.0 (Tamura *et al*. 2007). Using the Kimura two parameter (K2P) distance model (Kimura 1980), within and between group distance values were calculated and a neighbour-joining tree was constructed to give a graphical representation of divergence patterns between species. Bootstrapping was performed with 1,000 replications.

Specimens examined are deposited at the British Museum of Natural History, London (BMNH); Australian National Fish Collection, Hobart, Australia (CSIRO); Sabah Museum Elasmobranch Collection, Kota Kinabalu, Sabah, Malaysia (SMEC); Institut Penyelidikan Perikanan Sarawak/Sarawak Fisheries Research Institute, Kuching, Malaysia (IPPS or SFRI); Institut Penyelidikan Marin Borneo, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia (IPMB); Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB); and Zoological Reference Collection, National University of Singapore, Singapore (ZRC). Field accession numbers for specimens collected on the NSF elasmobranch project (NSFEP) in Borneo which were photographed, but not retained, and/or had tissue removed are prefixed with the letters KA or BO (data and images for these specimens are available at http://tapeworms.uconn.edu). Comparative material of other *Pastinachus* species is extensive, and is based on field specimens, and material referred to in published and unpublished manuscripts prepared by the authors.

FAMILY DASYATIDAE

Genus *Pastinachus* Rüppell, 1829

Type species. *Raja sephen* Forsskål 1775, by subsequent designation

SPECIES.– *Pastinachus* presently includes four valid nominal species: *P. atrus* (Macleay, 1883), *P. gracilicaudus* sp. nov., *P. sephen* (Forsskål, 1775), and *P. solocirostris* Last, Manjaji & Yearsley, 2005. A fifth un-named taxon is described in a following paper of this publication.

Pastinachus gracilicaudus sp. nov.

Figs 1–3, 5a, 6a,b, 7a, 8; Table 1

Holotype. SMEC 35 (previous field no. BKK 35), immature male 364 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 19 Apr. 1996.

Paratypes. 25 specimens: BMNH 1867.11.28.168, immature male 236 mm DW, probably Indonesia (purchased by Bleeker on 30 Jul. 1847); BMNH 1926.12.21.1, immature male 225 mm DW, Borneo; CSIRO H 4213–02, female (tail only retained), Sandakan market, Sabah, Malaysia, 04 Apr. 1996; CSIRO H 4426–28, immature male 403 mm DW, Jakarta, Muara Angke market, Indonesia, 17 Oct. 1995; CSIRO H 5480–03, immature male 309 mm DW, Sandakan fish market, Sabah, Malaysia, 29 Mar. 1999; CSIRO H 5612–02, immature male 193 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 20 Apr. 1999; CSIRO H 5615–03, female 318 mm DW, Sandakan fish market, Sabah, Malaysia, 24 Apr. 1999; CSIRO H 5864–03, immature male 342 mm DW, CSIRO H 5864–04, female 418 mm DW, Miri fish market, Sarawak, Malaysia, 24 May 2002; CSIRO H 7107–01, adult male 695 mm DW, Pesanguan Kanan, West Kalimantan, Indonesia, 02°02′ S, 110°07′ E, 15 Jul. 2007; CSIRO H 7108–01, adult male 650 mm DW, Sukanabanung, West Kalimantan, Indonesia, 01°48′ S, 109°57′ E, 16 Jul. 2007; CSIRO H 7109–01, female embryo 165 mm DW (pup of CSIRO H 7109–02), CSIRO H 7109–02, female (tail only retained, mother of CSIRO H 7109–01), Sandakan fish market, Sabah, Malaysia, 22 Apr. 1999; IPMB 38.01.09, female embryo 266 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 08 Aug. 2004; IPMB 38.01.10, sex unknown 670 mm DW (tail only retained), IPMB 38.01.11, female 475 mm DW (tail only retained), Kota Kinabalu fish market, Sabah, Malaysia, 31 Aug. 2004; IPMB 38.09.09, immature male 206 mm DW, Sandakan fish market, Sabah, Malaysia, 22 Apr. 1999; IPMB 38.09.10, male embryo 261 mm DW, Sandakan fish market, Sabah, Malaysia, 25 Apr. 1999; IPMB 38.09.12, immature male 363 mm DW Sandakan fish market, Sabah, Malaysia, 28 Mar. 1999; MZB 18227 (KA 162A), female embryo 253 mm DW, Selakau, West Kalimantan, Indonesia, 01°03′ N, 108°58′ E, 11 Jul. 2007; SFRI 27404–2, immature male 505 mm DW, Mukah fish market, Sarawak, Malaysia, 27 Apr. 2004; SFRI 28404–15, adult male 747 mm DW, Mukah fish market, Sarawak, Malaysia, 28 Apr. 2004; ZRC 50645 (3 specimens) immature males 304, 305 mm DW and female 316 mm DW, Jurong Fishery Port, Singapore (collected from either Andaman Sea or South China Sea), Feb. 1997.

Other material. 3 specimens: CSIRO H 4122–04, female 330 mm DW, off Beruwala, Sri Lanka, 06°29′ N, 79°59′

Figure 1. *Pastinachus gracilicaudus* sp. nov., juvenile male holotype (SMEC 35, 364 mm DW, preserved): dorsal surface.

E, 24 Apr. 1993; NSFEP KA 162 (not retained), female 830 mm DW, Selakau, West Kalimantan, Indonesia, 01°03′ N, 108°58′ E, 11 Jul. 2007; NSFEP KA 387 (not retained), immature male 358 mm DW, Sukadana, West Kalimantan, Indonesia, 01°14′ S, 109°57′ E, 17 Jul. 2008.

DIAGNOSIS.— A medium-sized species of *Pastinachus* (attaining about 75 cm DW) with the following combination of characters: snout rounded, not produced, angle exceeding 115°, apex largely naked and lacking enlarged denticles; disc length 83–89% DW; head length 38–41% DW; preoral length 15–17% DW; distance between nostrils 7–8% DW; distance between first gill slits 18–20% DW; tail compressed above mid-base of ventral cutaneous fold, width 0.5–0.8 times its height; ventral fold low and slender, its length 0.7–1.0 times DW, 17–22 times its depth below its mid-base, depth 2.0–3.6 times tail height at its mid-base; distance from anterior cloaca to sting 0.8–1 in precloacal length; two large, midscapular pearl thorns, usually preceded by a smaller irregular thorn; pectoral-fin radials 120–122; monospondylous vertebral centra (exc. synarcual) 37–40.

DESCRIPTION.— Disc of holotype weakly rhomboidal to rounded, obtuse anteriorly, not produced anteriorly; slightly longer than broad, length 1.15 times width in holotype (1.05–1.21 in non-embryological paratypes); axis of greatest width over or slightly in advance of mid-scapular thorns, its distance from snout tip 1.76 (1.78–1.94) times distance from tip of snout to pectoral-fin insertion; strongly elevated above cranium, thickest above mid-scapular region, maximum body depth 16.0% (13.3–17.8%) of disc width; snout obtuse and short (not angular and elongate) with a small, but well-defined, apical lobe; apical lobe broadly triangular, its tip bluntly rounded and subequal to eye diameter; snout angle 122° (117–121°); anterior margin of disc weakly convex anteriorly, more strongly convex near pectoral-fin apex; apex broadly rounded (becoming more acute in adult paratypes); posterior margin broadly convex, more convex posteriorly than anteriorly; free rear tip narrowly rounded. Pelvic fin subtriangular, well developed, its length 22.6% (20.5–23.7%) DW, 1.25 (1.01–1.50) times width across pelvic-fin base; anterior and posterior margins almost straight; apex and inner margin narrowly rounded. Clasper large, conical, pointed distally; adult postcloacal clasper length 21.2–26.3% DW (n=3), immature clasper 11.5–14.3% DW (n=7); distal length from pelvic axil 13.8–14.1% DW in adults.

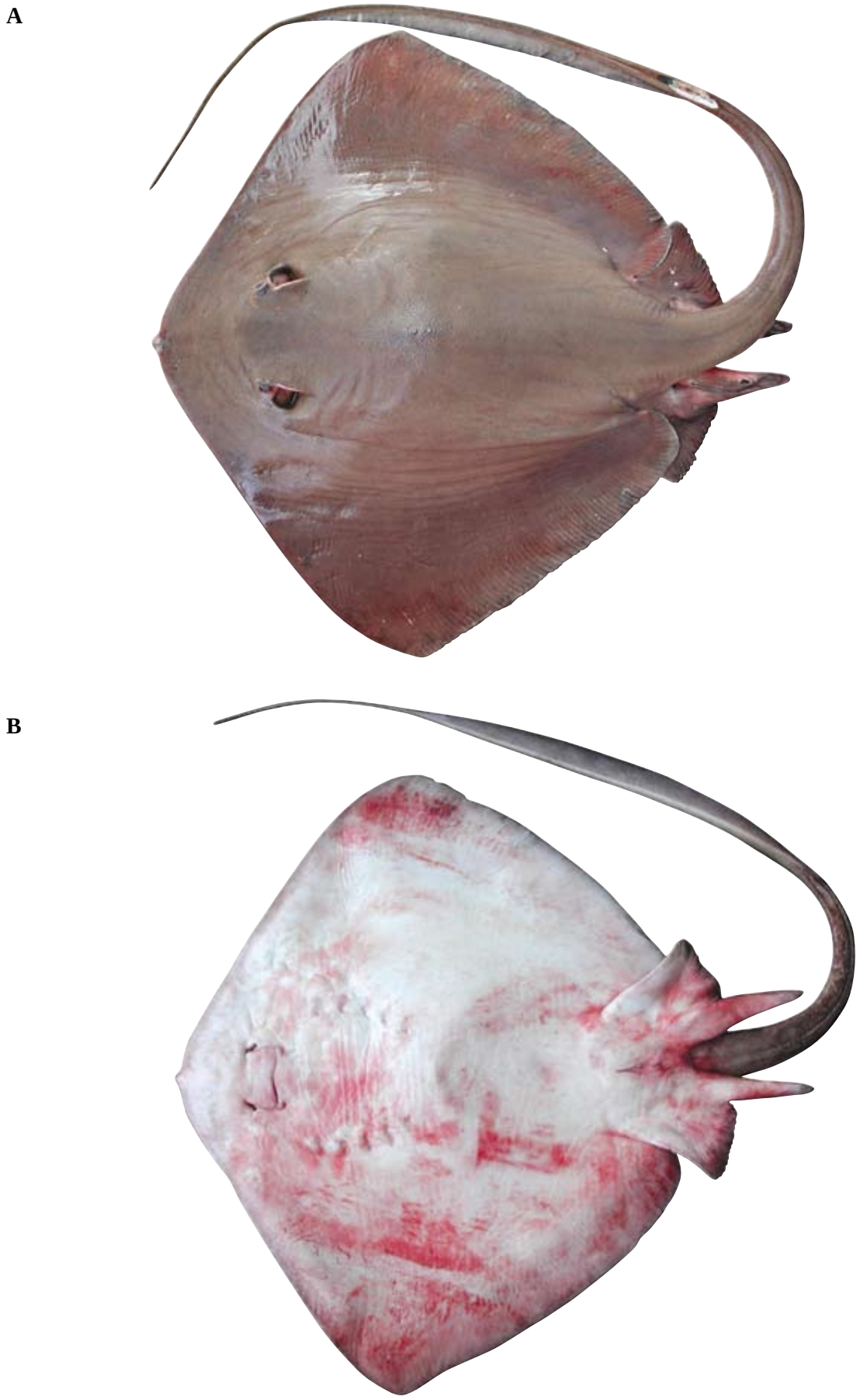

Figure 2. *Pastinachus gracilicaudus* sp. nov., adult male paratype (SFRI 28404–15, 747 mm DW, fresh): A. dorsal surface; B. ventral surface.

Table 1. Body proportions expressed as percentages of disc width for the holotype (SMEC 35) and 19 paratypes of *Pastinachus gracilicaudus* sp. nov.

		Paratypes					
		adults & immatures			embryos & neonates		
		n=14			n=5		
	Holotype	Min.	Max.	Mean	Min.	Max.	Mean
Disc, width (mm)	364	304	747		165	266	
Total length	265.7	246.5	334.1	297.4	334.6	365.8	353.3
Disc, length (direct)	86.8	82.6	88.5	85.8	84.6	95.2	89.1
Disc, thickness	16.0	13.3	17.8	16.1	15.5	17.0	16.5
Disc, end of orbit to pectoral insertion	56.1	49.5	56.5	53.7	54.5	59.8	57.3
Disc, snout to maximum width	43.5	38.2	43.7	41.3	40.2	45.5	43.1
Head length (direct)	40.4	38.2	40.9	39.7	40.1	44.5	42.3
Snout, preorbital (direct)	19.4	18.1	20.8	19.2	18.9	19.6	19.2
Snout, preoral (direct)	16.5	15.1	16.7	15.9	16.3	18.4	17.3
Snout, prenasal (direct)	12.3	11.7	13.5	12.7	12.6	12.9	12.8
Orbit diameter	4.1	3.2	5.0	4.0	4.6	6.5	5.7
Eye diameter	2.6	1.8	3.1	2.4	2.9	4.5	3.7
Inter-eye width	18.6	14.1	17.5	15.9	18.0	19.3	18.7
Orbit and spiracle length	9.3	7.7	9.8	8.7	9.7	12.4	11.0
Spiracle length	7.2	5.9	7.5	6.6	6.4	9.5	8.2
Interspiraclar width	17.6	14.3	17.6	16.1	18.0	20.9	19.8
Mouth width	8.9	7.4	8.6	8.1	7.7	9.4	8.6
Nostril length	3.3	2.5	3.1	2.8	2.8	3.5	3.1
Nasal curtain, length	6.0	4.7	5.9	5.2	5.1	5.5	5.3
Nasal curtain, width	10.6	9.4	10.7	9.8	9.5	10.8	10.2
Internasal width	8.0	6.8	7.7	7.4	7.8	8.8	8.2
Width, 1st gill slit	3.2	2.8	3.3	3.0	2.8	3.9	3.1
Width, 5th gill slit	2.2	2.2	2.6	2.4	2.0	2.4	2.1
Distance between 1st gill slits	20.3	17.8	20.4	19.2	19.8	21.2	20.6
Distance between 5th gill slits	13.3	12.2	13.5	12.7	13.0	14.2	13.6
Pelvic fin, length	22.6	20.5	23.7	22.4	20.8	24.0	22.7
Pelvic-fin base, width	14.8	17.6	18.6	18.1	16.0	18.4	17.6
Tail width, axil of pelvics	9.2	9.1	11.2	10.2	9.4	12.5	10.8
Tail height, axil of pelvics	5.9	5.7	7.2	6.4	5.6	7.4	6.5
Tail width, base of sting	3.3	2.7	3.8	3.1	2.9	3.9	3.5
Tail height, base of sting	2.8	2.7	3.2	2.8	3.0	3.2	3.1
Ventral fold, length	81.9	74.0	103.5	90.9	90.6	108.8	99.8
Tail filament length	41.4	27.4	89.4	56.7	30.3	112.1	86.5
Tail width, fold origin	4.4	3.0	4.2	3.7	3.6	4.9	4.1
Tail depth, fold origin	3.0	2.6	3.4	2.9	2.8	3.3	3.1
Tail width, at 25% base length of fold	1.7	1.6	2.4	2.0	1.8	2.7	2.2
Tail depth, at 25% base length of fold	2.0	1.8	2.3	2.0	2.0	2.5	2.3
Fold depth, at 25% of its base length	3.4	2.3	3.8	3.1	2.3	3.8	2.7
Tail width, at mid-base length of fold	1.1	1.0	1.3	1.1	0.9	1.3	1.2
Tail depth, at mid-base length of fold	1.3	1.3	2.0	1.7	1.4	2.0	1.8
Fold depth, at its mid-base	4.4	3.9	5.6	4.6	3.5	5.5	4.4
Tail width, at 75% base length of fold	0.7	0.6	1.1	0.8	0.7	1.0	0.9
Tail depth, at 75% base length of fold	0.8	0.8	1.5	1.1	1.2	4.2	1.9
Fold depth, at 75% of its base length	3.9	3.0	5.9	4.2	2.9	4.9	3.8

Table 1. cont'd.

		Paratypes					
		adults & immatures			embryos & neonates		
		n=14			n=5		
	Holotype	Min.	Max.	Mean	Min.	Max.	Mean
Tail width, insertion of fold	0.6	0.5	1.1	0.7	0.6	1.0	0.8
Tail depth, insertion of fold	0.7	0.5	0.9	0.7	0.8	1.1	1.0
Fold origin-sting origin, length	6.7	3.5	8.3	5.5	4.2	7.6	5.7
Sting length	–	–	–	–	15.5	15.5	15.5
Snout to origin of cloaca	73.0	68.9	73.4	71.4	72.1	76.2	73.7
Cloaca origin to sting	73.5	68.6	83.2	76.9	76.3	82.7	79.1
Cloaca origin to tail tip	192.6	175.9	260.7	226.1	262.5	358.8	298.0
Cloaca length	7.1	6.0	7.7	6.8	6.4	7.9	6.8
Clasper, postcloaca length	12.4	11.5	26.3	17.3	11.6	12.0	11.8
Clasper, length from pelvic axil	3.6	3.9	14.1	8.3	4.1	5.1	4.6

Tail moderately elongate, postcloacal tail 2.64 (2.49–3.55) times precloacal length; its base depressed (increasingly more so in adults), width 1.61 (1.34–1.96) times height, almost flat to weakly convex above and below, narrowly rounded laterally; tapering strongly and evenly to sting, width 1.44 (1.07–1.72) times height at ventral skin fold origin; subcircular to slightly compressed in cross-section at end of sting; dorsal surface behind sting with a deep, naked groove; at mid-fold, compressed, oval, width 0.80 (0.54–0.75) times height; at end of fold, slightly depressed, rhomboidal to rounded; becoming filamentous and more depressed towards its tip; very narrow (but obvious) mid-lateral skin fold extending along anterior margin of tail, originating near pelvic-fin rear tips and extending posteriorly for about distance between first gill slits. Ventral skin fold relatively slender, its length 1.22 (0.97–1.20) in disc width, 2.35 (2.09–2.83) in postcloacal tail, 0.90 (0.78–0.89) in distance from cloaca to sting origin, 18.6 (16.9–22.5) times its depth at its midlength; its depth, 1.73 (1.20–2.36) at anterior quarter of its length, 3.32 (2.02–3.62) at its mid length, and 4.71 (2.89–5.91) at its posterior quarter, times height of adjacent part of tail; its origin 6.7% (3.5–8.3)% DW forward of sting origin; terminal portion of fold rarely terminating abruptly, usually graduating evenly toward tail and continuing more than orbit diameter along tail as a low barely detectable ridge; distance from anterior cloaca to sting origin 0.99 (0.82–1.01) of precloacal length, 0.85 (0.83–0.98) of disc length; tail filament (post-fold length) 1.98 (1.01–3.03) in fold length, 4.65 (2.87–6.41) in tail length.

Snout relatively short, not greatly depressed posteriorly, preoral length 1.85 (1.75–2.05) times mouth width, 2.06 (2.00–2.31) times internarial distance, 0.81 (0.77–0.88) in distance between first gill slits; direct preorbital snout length 1.57 (1.34–1.72) times interorbital length; distance from snout to level of maximum disc width 2.30 (2.29–2.62) in DW; interorbital space very broad, flat to slightly convex; eyes small, dorsolateral, elevated slightly and protruding laterally and dorsally, orbit diameter 1.75 (1.43–1.91) in spiracle length, eye diameter 2.77 (2.06–3.16) in spiracle length; interorbital distance 2.98 (2.47–3.85) times orbit diameter, intereye 7.12 (4.33–7.91) times eye diameter. Spiracles suboval to subquadrangular, greatly enlarged, situated dorsolaterally. Nostril slit-like, oblique, directed posterolaterally; anterior margin fleshy, anterior nasal fold reduced, membranous, abutting internasal flap anteriorly; posterior lobe broad, fleshy, largely concealed beneath nasal curtain; internasal distance 1.53 (1.58–1.78) in prenasal length, 2.47 (2.45–3.02) times nostril length. Nasal curtain weakly to moderately bilobed, relatively broad, short, flat, lacking an obvious longitudinal medial groove, weakly papillose, width 1.75 (1.77–2.24) times length; posterolateral apex partly recessed within broad submarginal groove of posterior nasal flap; anterior lateral margin concave, smooth edged; apex narrowly and evenly rounded; posterior margin finely fringed, moderately concave medially; covering most of mouth, including symphysis of lower jaw in holotype.

Mouth not greatly protrusible; skin on chin fleshy, weakly papillose; anterior floor with 1+3+1 oral papillae (in paratypes IPMB 38.09.09 and CSIRO H 5480–03), three central papillae almost coalesced basally, slightly taller than those laterally; posterior floor with three, low, parallel buccal ridges; oral curtain broad; roof with three, well-developed palate ridges, converging anteriorly, coinciding with oral papillae with mouth closed. Upper jaw extremely strongly arched at all stages of growth, barely moveable; symphysial part of jaw directed poster-oventrally, outer labial teeth forming a perpendicular angle with anterior labial teeth; posterior lingual teeth almost perpendicular with those of symphysis of upper jaw;

mid-lateral median teeth forming a bulbous arch. Lower jaw plate-like, subtriangular, moveable, symphysial teeth visible ventrally on jaw, protruding slightly, fully recessible into anterior arch of upper jaw. Teeth variable in size in jaws, moderately large to small, difficult to access in preserved material without dissection; largest in mid-lateral region of upper jaw, smallest near symphysis of upper jaw; crowns hexagonal, without cusps, close set, quincuncial; in CSIRO H 5480–03, rows in upper jaw 29; rows in lower jaw 20.

Gill openings S-shaped, forming unfringed lobes laterally; length of first gill slit 1.47 (1.10–1.44) times length of fifth gill slit, 2.81 (2.44–3.35) in mouth width; distance between first gill slits 2.52 (2.44–2.76) times internasal distance, 0.50 (0.47–0.53) of ventral head length; distance between fifth gill slits 1.65 (1.62–1.89) times internasal distance, 0.33 (0.30–0.35) of ventral head length.

Dorsal disc broadly covered in a wide denticle band (and with thick mucus in fresh specimens); narrow naked region (subequal or slightly wider than orbit diameter) extending around anterior disc margin to about hind level of spiracle, becoming broadest adjacent pectoral-fin apex (subequal to or slightly wider than snout length), then extending broadly posteriorly to pelvic-fin insertion; pelvic fins and claspers naked; immediate preorbit, suborbit and inner spiracle naked. Scapular region dominated by 2, greatly enlarged, pearl-shaped thorns; a third, smaller and more irregular thorn preceding pearl thorns in most paratypes (absent in holotype); width of largest pearl thorn 1.6% DW (relatively smaller in adult paratypes, 0.7–0.9% DW), narrowly separated from other pearl thorn by about half length of first thorn (more widely separated in adult paratypes, by about 1.5 times length of first thorn); denticles on mid disc and interorbital space distinctly larger than those laterally, also mostly slightly more widely spaced; denticles becoming progressively smaller towards lateral margin of band; lateral margin of band with variable, longitudinal denticle rows, often separated by narrow naked strips in paratypes; denticles at snout margin distinctly larger than those along lateral margin, not greatly enlarged or cuspid; margin of denticle band somewhat truncate preceding pectoral-fin insertion; present on distal edge of spiracle (extending into spiracle in adult paratypes); most of dorsal surface of tail covered with denticles at its base; tail band extending posteriorly to pelvic-fin insertions (along full length of tail in largest paratypes); entire midline of tail behind skin-fold origin scaled, rest of tail naked; in adult males, most of tail covered with small denticles (usually absent near base of skin fold), no enlarged denticles along dorsal midline; tail fold mostly smooth with fine longitudinal striae, sometimes with a very sparse scattering of denticles. Main denticles typically stellate, crowns raised slightly, flat topped; ventral surface of disc and tail before ventral fold naked. Most specimens have stinging spine removed; length of sting in one embryo paratype (CSIRO H 7109–01) 15.5% DW. Lateral line not obvious on ventral surface.

Figure 3. Ventral view of the oronasal region of *Pastinachus gracilicaudus* sp. nov., adult male paratype (SFRI 28404–15, 747 mm DW, fresh).

Meristic data were obtained for 6 paratypes: total pectoral-fin radials 120–122, propterygium 50–52 (non-type 53), mesopterygium 14–17 and metapterygium 51–56. Total pelvic-fin radials of immature males 23–25 (n=3), females 29–30 (n=3). Total vertebral centra 168–178 (exc. synarcual), cranial segments 5–6, postcranial monospondylous centra 37–40, diplospondylous centra 131–139.

COLORATION.— When fresh (based on paratypes): Dorsal surface of disc and tail uniformly greyish brown, typically with a reddish or purplish hue; often slightly darker, almost blackish along dorsal midline of tail behind sting; pelvic fins and dorsal clasper similar to outer disc (more reddish than central disc); dorsal margin of spiracles and preorbit whitish; anterior disc with very narrow, pale margin. Ventral surface of disc uniformly pale, outer margin narrowly dusky to blackish, similar on posterior margin of pelvic fin, and tip of clasper in adult males; tail dark brownish before skin fold, paler near its base, yellowish to white above skin fold, becoming darker on filament; ventral skin fold base whitish, grading to dusky medially and blackish along its outer margin. In preservative: Holotype uniform medium brownish dorsally, slightly paler near outer disc margin with lighter areas on tail; pearl thorns prominent, whitish. Ventral surface of disc and pelvic fins uniformly white; tail dark brownish, lighter anteriorly; skin fold pale greyish brown.

Figure 4. *Pastinachus atrus*, immature male (NSFEP KA 389, 835 mm DW, fresh): dorsal surface.

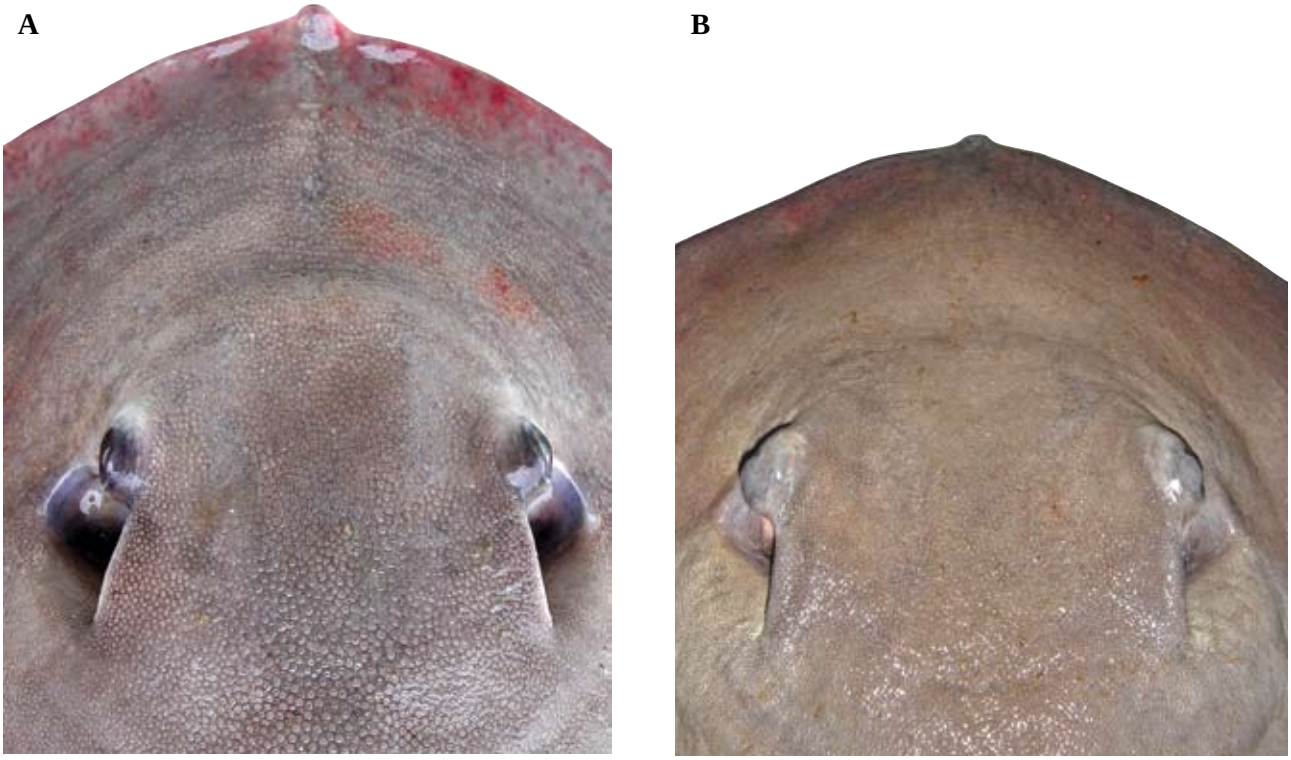

Figure 5. Head shape and patterns of squamation of: A. *Pastinachus gracilicaudus* sp. nov., immature male paratype (SFRI 27404–02, 505 mm DW, fresh); B. *P. atrus*, immature male (NSFEP KA 389, 835 mm DW, fresh).

SIZE.— Largest specimen a female 830 mm DW, largest adult male 747 mm DW, largest immature male 505 mm DW; a 695 mm DW adult male (CSIRO H 7107–01) weighed ca 12 kg. Size at birth apparently variable; an 830 mm DW female (NSFEP KA 162) delivered a full term embryo (MZB 18227, 253 mm DW) with small umbilical scar; however, other retained specimens, IPMB 38.09.10 (261 mm DW) still had a substantial yolk sac, but in CSIRO H 5612–02 (193 mm DW) the umbilical scar was barely visible. All of these young specimens have large mid-scapular tubercles and well-developed denticles over most of the dorsal disc; a small embryo with yolk sac (CSIRO H 7109–01, 165 mm DW) has prominent mid-scapular tubercles, but other denticles are just starting to form on the disc.

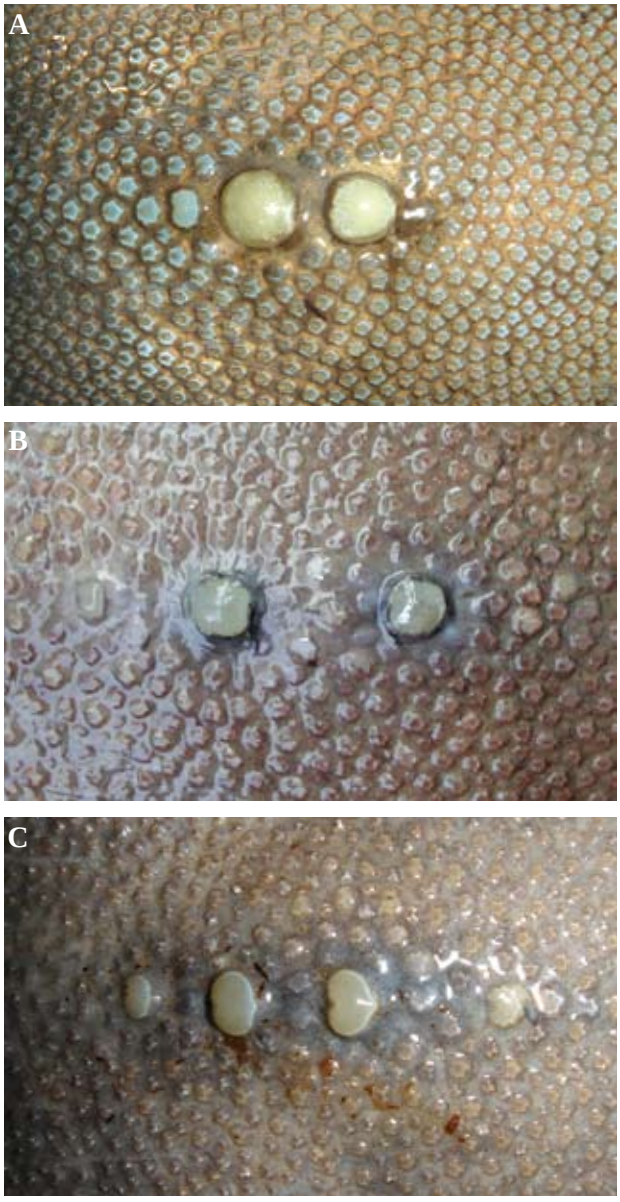

Figure 6. Patterns of squamation in the mid-scapular area of: A. *Pastinachus gracilicaudus* sp. nov., immature male (NSFEP KA 387, 358 mm DW, fresh); B. *P. gracilicaudus* sp. nov., adult male paratype (SFRI 28404–15, 747 mm DW, fresh); and C. *P. atrus*, immature male (NSFEP KA 389, 835 mm DW, fresh).

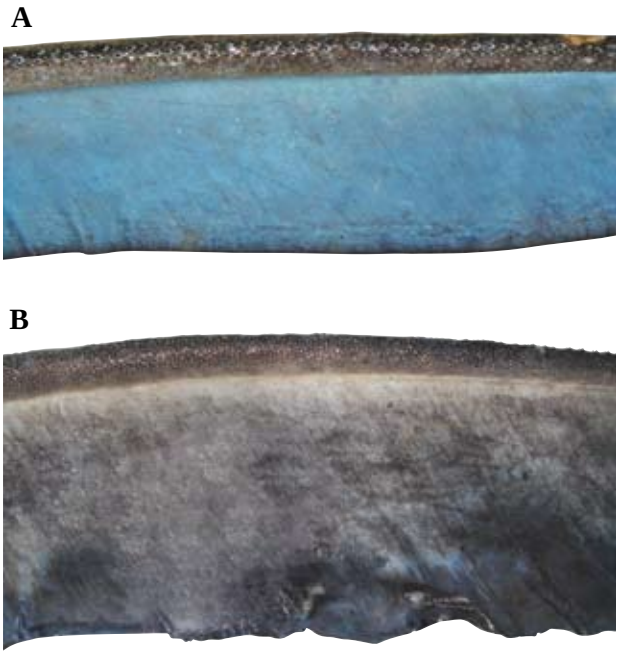

Figure 7. Lateral view through the tail at the mid region of the ventral cutaneous fold of: A. *Pastinachus gracilicaudus* sp. nov., immature male (NSFEP KA 387, 358 mm DW, fresh); B. *P. atrus*, immature male (NSFEP KA 389, 835 mm DW, fresh).

ETYMOLOGY.— Derived from a combination of the Latin *gracilis* (slender, thin) and *cauda* (tail, appendage) in allusion to the slender appearance of the tail and narrow ventral cutaneous fold, compared to other members of the genus *Pastinachus*. Vernacular: Narrowtail Stingray.

DISTRIBUTION.— Reasonably common but patchily distributed in both Malaysian and Indonesian Borneo, including Sabah, Sarawak, and western and northeastern Kalimantan (see Fig. 9). Locality details for specimens collected at fish markets in Singapore and Jakarta are unknown. Possibly more widespread in the Indo–Malay Archipelago, east to at least the Wallace Line; the identity of a specimen collected off Beruwala (Sri Lanka) needs confirmation. Presently confused with other species of *Pastinachus* so its distribution needs to be better defined. Depth unknown as most material collected in fish markets, probably mainly coastal.

COMPARISONS.— Of the four species of *Pastinachus*, *P. gracilicaudus* most closely resembles *P. atrus* (sympatric with it in the Indo–Malay Archipelago, Figs 4, 5b) and *P. sephen* in body shape by having a generally broad disc with an obtusely rounded snout tip and acute pectoral-fin apices. However, apart from being a much

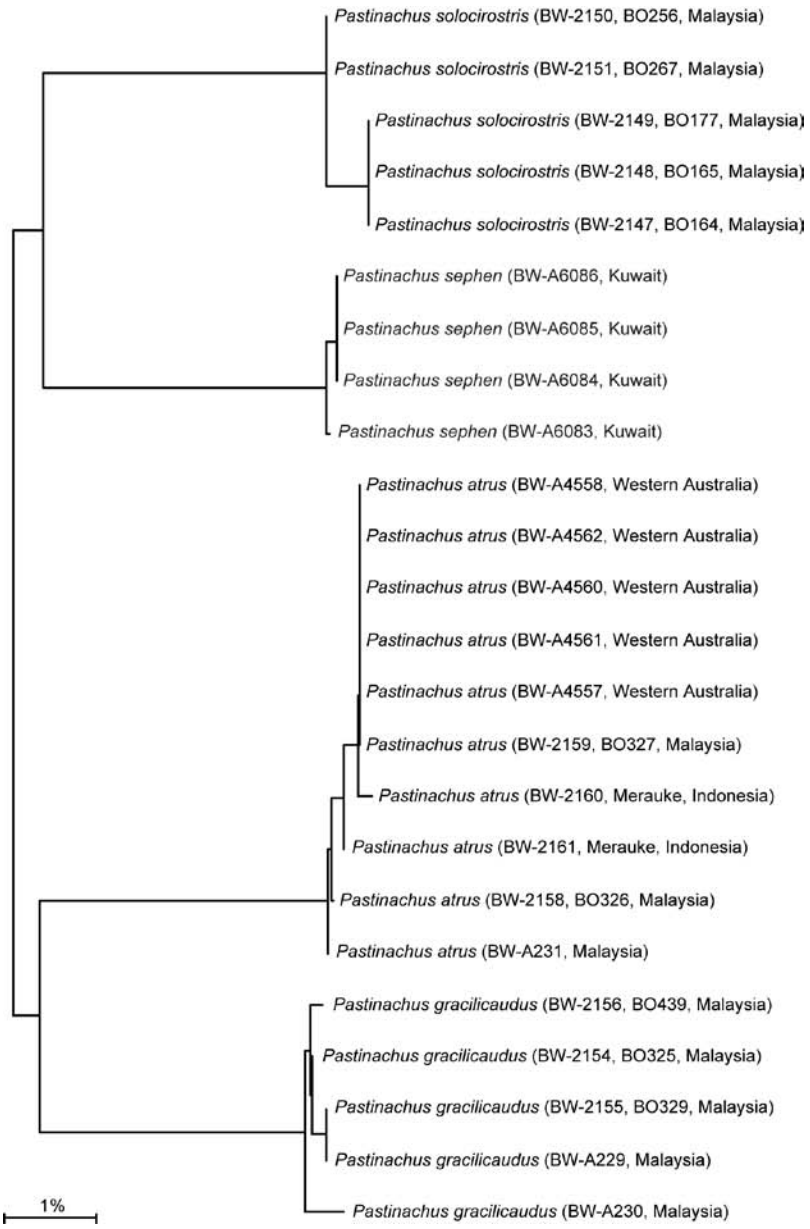

Figure 8. Neighbour-joining tree of nucleotide sequence divergence at the barcoding region of the COI gene among four species of the genus *Pastinachus*. Scale bar represents 1% K2P distance and bootstrap values of ≥75% are given. Registration numbers relate to those present on the Barcode of Life Database (www.barcodinglife.org).

smaller species (attaining about 75 cm DW vs. almost 200 cm DW (Last & Stevens, 2009), *P. gracilicaudus* differs in mid-scapular denticle morphology (having large, bulbous, pearl thorns rather than smaller and lower heart-shaped thorns, Fig. 6), and a more slender ventral tail fold (depth at its midlength 2.8–3.6 vs. 3.6–5.7 times tail height at the same location on the tail in specimens exceeding 50 cm DW, Fig. 7). These species differ in their COI barcode sequences (see Fig. 8), and in several other morphometric characters presently under investigation by one on us (PL).

Pastinachus gracilicaudus is also sympatric with another smaller congener, *P. solocirostris* (attaining about 45 cm DW). These species have notably different body shapes and anterior denticle morphology. The disc of *Pastinachus gracilicaudus* is less broad, the snout is rounded and not produced (vs. angular in *P. solocirostris*) and its angle is more obtuse (117–122° vs. 92–109°), and the snout tip is largely naked and lacks enlarged denticles (vs. spiny with enlarged lanceolate denticles).

Pastinachus species appear to differ considerably

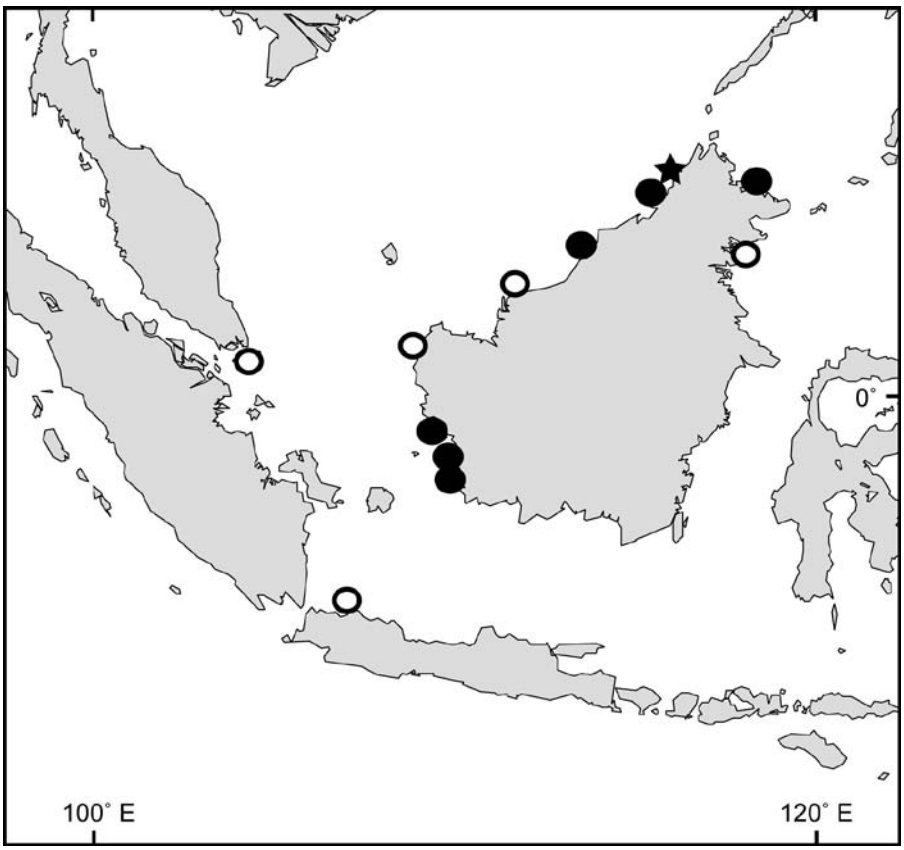

Figure 9. Distribution of *Pastinachus gracilicaudus* sp. nov. in the Western Central Pacific. Solid star represent the holotype locality, solid circles paratypes with known locality and open circles paratypes collected from fish markets without exact capture locality information or other specimens not retained.

in body proportions and meristics. The two species comprehensively described to date, *P. gracilicaudus* and *P. solocirostris*, have non-overlapping differences in several morphometric characters: disc length 83–89% DW in *P. gracilicaudus* (vs. 94–101% DW in *P. solocirostris*), head length 38–41% DW (vs. 47–51% DW), preoral length 15–17% DW (vs. 21–25% DW); distance between nostrils 7–8% DW (vs. 9–11% DW), distance between first gill slits 18–20% DW (vs. 20–25% DW), and length of ventral tail fold 0.7–1.0 (vs. 1.1–1.3) times DW and 17–22 (vs. 32–41) times its depth below its mid-base. Similarly, there are 120–122 pectoral-fin radials in *P. gracilicaudus* (vs. 113–120 in *P. solocirostris*), and 37–40 monospondylous vertebral centra (vs. 35–38).

DISCUSSION

Pastinachus gracilicaudus is sympatric in Borneo with *P. atrus*, *P. solocirostris* and another undescribed species, treated in this special publication on elasmobranchs from the Borneo region. These species differ markedly and it is surprising that they have been only recently recognised as distinct from each other. The support of molecular analysis has been important in providing supplementary evidence of their non-conspecificity. However, despite our improved knowledge of their identity, better information is needed on their distribution outside Borneo.

The morphometric data used to describe *P. gracilicaudus* is based on a conservative sample size and does not fully encapsulate intraspecific variability within this species. However, some characters appear to be allometric. For example, embryos and neonates are relatively longer (total length 247–334%, mean 297% in adults and immatures vs. 335–366%, mean 353% DW in embryos and neonates), with larger pearl thorns (width of largest thorn 0.7–1.9%, mean 1.3% vs. 2.2–3.3%, mean 2.6% DW), eyes (diameter 1.8–3.1%, mean 2.4% vs. 2.9–4.5%, mean 3.7% DW), combined orbit and spiracle lengths (7.7–9.8, mean 8.7% vs. 9.7–12.4%, mean 11.0% DW), and interspiracular distances (14.3–17.6%, mean 16.1% vs. 18.0–20.9%, mean 19.8% DW). Despite this intraspecific variability, morphometrics are useful in distinguishing species of this genus.

Molecular techniques provided equally good discrimination of species. Specimens of *P. gracilicaudus*

had almost identical barcode sequences that differed greatly from those of three congeners, *P. atrus*, *P. sephen* and *P. solocirostris* (Fig. 8). All taxa exhibited 100% bootstrap support and low average within species divergence but high overall average divergence separating species (R. Ward, pers. comm.). High levels of species separation are consistent with those found in other confamilial stingray groups, such as genera *Dasyatis* and *Himantura* (Ward *et al*., 2008), and support the repro-ductive isolation of *P. gracilicaudus* from its congeners.

In the last half a decade, the genus *Pastinachus* has gone from being a monotypic genus to being a species complex. A full revision of the group, which will provide a comparison and redescription of *P. atrus* and *P. sephen*, is presently in progress (Last, in prep.). Additional forms and nominal species exist in the Indian Ocean that need to be resolved in the light of information provided here.

Comparative material (referred to in paper):
Pastinachus atrus: NSFEP KA 389 (not retained), immature male 835 mm DW, Pesanguan Kanan, West Kalimantan, Indonesia, 02°02′ N, 110°07′ E, 18 Jul. 2008.

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Pastinachus stellurostris sp. nov., a new stingray (Elasmobranchii: Myliobatiformes) from Indonesian Borneo

Peter R. Last[1], Fahmi[2] & Gavin J.P. Naylor[3]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Research Centre for Oceanography, Indonesian Institute of Sciences (LIPI), Jl. Pasir Putih I, Ancol, Timur Jakarta 14430, INDONESIA
[3] Florida State University, School of Computational Science/Department of Biological Science, Tallahassee, FL 32304, USA

ABSTRACT.— A new dasyatid stingray, *Pastinachus stellurostris* sp. nov., is described from a few specimens collected from Indonesian Borneo, near Pontianak (West Kalimantan). It shares with *P. solocirostris*, which occurs in the same bioregion, a similar disc shape and a spiny, angular snout. The first specimen collected was initially confused with *P. solocirostris* until molecular analysis indicated that two related species exist in the region. *Pastinachus stellurostris* can be distinguished from *P. solocirostris* in having broad, star-shaped (rather than narrow and lanceolate) denticles on the snout and a row of well-developed thorns along the mid-line of the back and tail (otherwise absent). It also differs slightly in disc morphometry and has a more slender ventral tail fold. This species was not collected in other recent surveys of Indo-West Pacific elasmobranchs, including eastern Indonesia, and its confirmed range is confined to the brackish/freshwater habitats of the Kapuas River estuary and in coastal parts of western Borneo. A similar ray collected in freshwater in the Bang Pakong River (Thailand) may be conspecific with this species.

Key words: *Pastinachus stellurostris* – new species – stingray – Dasyatidae – Borneo – Indonesia

PDF contact: john.pogonoski@csiro.au

INTRODUCTION

In July 2007, an adult male specimen of a new species of cowtail ray was collected at Sungai Kakap fish market near Sepuk Laut (Kalimantan) by an international research team led by Dr. Janine Caira during a survey of the biodiversity the Borneo chondrichthyans and their parasites. This species was initially misidentified by the field team as the Roughnose Stingray, *Pastinachus solocirostris* Last Manjaji & Yearsley, 2005, due to its strikingly similar morphology to that species, particularly in its relatively elongate disc and very angular, spiny snout. *Pastinachus solocirostris* is reasonably common in this bioregion so this specimen was dissected for parasites and discarded. Fortunately, due to the rigorous field collecting procedures adopted by the parasite team, where detailed images and tissue samples are taken from all potential parasite hosts dissected, important details of the morphology of this ray were retained. Molecular analysis by one of us, Gavin Naylor, later demonstrated that this specimen was not conspecific with *P. solocirostris*. This finding led to detailed scrutiny by the senior author of the excellent series of images available of this specimen, confirming that these two rays were also morphologically distinct.

A second specimen, identified as *P. solocirostris*, was independently collected by another of us (Fahmi) in 2005 on an earlier field trip to Kalimantan. It was deposited in LIPI's elasmobranch collection (Ancol, Jakarta) where it was later re-examined and confirmed to be conspecific with our new stingray. In 2009, a search for additional type material yielded two other specimens, including the adult male holotype and a large female. This new cowtail stingray is described and named below.

METHODS

Characteristics of the disc (including squamation, tooth row counts and meristic counts) follow standards adopted by Compagno & Roberts (1982), Manjaji (2004), Last *et al*. (2006) and Manjaji-Matsumoto & Last (2006). Meristics were obtained from radiographs and morphometric methods generally follow Compagno & Heemstra (1984) and Last & White (2008). Additional characters were derived by Last *et al*. (2005) to account for characteristic features of the tail; the shape of the tail and its associated ventral skin fold are important in distinguishing different species of the genus *Pastinachus*

so tail widths and depth (height) were recorded at the origin and insertion of the skin fold, as well as at quartile intervals along its length. A paratype (CSIRO H 7110–01) was radiographed but meristic details were not available for other material due to difficulties in accessing all material from Indonesia. A non-type specimen (MTUF P 30003) from Thailand is included after the holotype in the meristics and in Table 1.

A total of 54 measurements, expressed as proportions of disc width (DW, see Table 1), were taken for the holotype and the two paratypes, as well as from another specimen from Thailand which is possibly conspecific. Molecular data has been extracted from a broader NADH analysis of the Borneo chondrichthyan fauna by G. Naylor, J. Caira and K. Jensen. In the molecular trees, field codes (prefixed by BO, BOD, CM, DF or KA) are provided for samples collected by Drs J. Caira and K. Jensen, and data and images for these specimens are available at http://tapeworms.uconn.edu.

Specimens examined are deposited at the Australian National Fish Collection, Hobart, Australia (CSIRO), the Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB), and the Tokyo University of Fisheries, University Museum, Tokyo, Japan (MTUF). Field accession numbers for specimens collected on the NSF elasmobranch project (NSFEP) in Kalimantan, which were photographed but not retained, are prefixed with the letters KA. The comparative material of other *Pastinachus* species is extensive, and is based on additional non-retained field specimens, and material referred to in published and unpublished manuscripts prepared by one or more of the authors.

FAMILY DASYATIDAE

Genus *Pastinachus* Rüppell, 1829

Type species. *Raja sephen* Forsskål 1775, by subsequent designation

SPECIES.— *Pastinachus* includes five valid nominal species: *P. atrus* (Macleay, 1883), *P. gracilicaudus* Last & Manjaji-Matsumoto, 2010, *P. sephen* (Forsskål, 1775), and *P. solocirostris* Last, Manjaji & Yearsley, 2005, and *P. stellurostris* sp. nov.

Figure 1. *Pastinachus stellurostris* sp. nov., adult male holotype (MZB 18226, 422 mm DW, preserved): dorsal surface.

Figure 2. *Pastinachus stellurostris* sp. nov., female paratype (NCIP 6338, 413 mm DW, preserved): ventral surface.

Pastinachus stellurostris sp. nov.

Figs 1–6, 7a, 8, 9, Table 1

Holotype. MZB 18226 (formerly NCIP 6339), adult male 422 mm DW, Sungai Pinyuh fish market, caught near Pemangkat (West Kalimantan), Indonesia, ca 01°10′ N, 108°58′ E, 05 Aug. 2009.
Paratypes. 2 specimens: CSIRO H 7110–01, adult male 415 mm DW, Flamboyan Market, Pontianak, West Kalimantan, Indonesia, 20 Oct. 2005; NCIP 6338, female 413 mm DW, collected with holotype.
Other material. 2 specimens: NSFEP KA 306 (specimen not retained), adult male 428 mm DW, near Sepuk Laut, West Kalimantan, Indonesia, 00°12′51.60″ S, 109°05′00.30″ E, 27 Jul. 2007; MTUF P 30003, immature male 235 mm DW, Bang Pakong River (ca 60 km from mouth), Thailand, 13 Nov. 1997.

DIAGNOSIS.— A relatively small *Pastinachus* with the following combination of characters: snout relatively acute, angle about 117°, covered to apex with enlarged denticles with broad stellate crowns; short pungent thorns along midline of tail before sting; nuchal thorns pearl shaped; disc length 93–98% DW; head length 44–45% DW; preoral length 19–20% DW; distance between nostrils about 8% DW; distance between first gill slits 19–21% DW; tail compressed above midbase of ventral cutaneous fold, width 0.6–0.9 times its height; ventral fold relatively long and very slender, its length 1.1 times DW, 52–62 times its depth below its midbase; ventral fold depth 1–1.4 times tail height at its midbase; distance from cloaca to sting 1–1.1 times precloacal length; pectoral-fin radials about 117; post-synarcual monospondylous vertebral centra about 36; ventral fold much paler basally than distally.

DESCRIPTION.— Disc quadrangular, anteriorly angular and slightly produced; width slightly longer than length, 1.06 times length in holotype (1.02–1.08 in paratypes); axis of greatest width of disc barely in advance of nuchal thorns, 2.08 (2.06–2.11) times in distance from tip of snout to pectoral-fin insertion; body thickness 6.37 (6.62–6.78) times in disc width, barely raised above cranium (marginally more so above nuchal area); anterior margin of disc weakly concave beside eye, almost straight before apex; pectoral apex broadly rounded, posterior margin moderately convex, free rear tip narrowly rounded. Pelvic fin subtriangular; anterior margin undulate, concave near base, convex medially,

Table 1. Body proportions expressed as percentages of disc width for the adult male holotype (MZB 18226) of *Pastinachus stellurostris* sp. nov., and ranges for two paratypes from Borneo and a non-type specimen from Thailand (MTUF P 30003).

		Paratypes (n=2)		MTUF
	Holotype	Min.	Max.	specimen
Disc, width (mm)	422	413	415	235
Total length	334.6	319.6	351.8	402.9
Disc, length (direct)	94.3	92.8	97.6	94.6
Disc, thickness	15.7	14.8	15.1	16.2
Disc, end of orbit to pectoral insertion	57.8	57.3	59.1	58.4
Disc, snout to maximum width	38.3	39.4	40.0	44.9
Head length (direct)	44.3	43.7	45.1	45.8
Snout, preorbital (direct)	20.7	20.8	22.4	22.4
Snout, preoral (direct)	19.0	19.3	19.5	19.9
Snout, prenasal (direct)	15.3	14.7	14.8	14.9
Orbit diameter	4.7	4.4	4.8	4.8
Eye diameter	2.5	2.6	2.8	3.0
Inter-eye width	15.7	15.8	16.6	17.5
Orbit and spiracle length	9.2	8.7	9.8	10.0
Spiracle length	6.5	6.5	7.7	7.1
Interspiraclar width	16.5	16.6	17.6	18.7
Mouth width	8.2	8.6	8.6	8.6
Nostril length	3.6	3.7	3.7	3.3
Nasal curtain, length	5.7	5.6	6.0	6.3
Nasal curtain, width	10.1	10.4	10.5	11.0
Internasal width	7.9	7.9	8.0	8.6
Width, 1st gill slit	3.1	3.0	3.1	3.3
Width, 5th gill slit	2.3	2.5	2.6	2.5
Distance between 1st gill slits	20.7	19.0	20.8	21.9
Distance between 5th gill slits	13.8	12.9	13.4	13.8
Pelvic fin, length	21.6	22.2	24.1	26.9
Pelvic-fin base, width	21.6	22.1	22.4	17.3
Tail width, axil of pelvics	11.9	11.7	11.8	11.5
Tail height, axil of pelvics	6.5	6.5	6.7	6.5
Tail width, base of sting	3.7	3.2	3.5	3.4
Tail height, base of sting	3.2	3.2	3.2	3.6
Ventral fold, length	110.2	109.9	111.6	123.4
Tail filament length	71.1	50.1	86.3	130.2
Tail width, fold origin	4.0	4.0	4.1	4.8
Tail depth, fold origin	3.1	3.0	3.2	3.7
Tail width, at 25% base length of fold	1.9	1.7	1.8	2.1
Tail depth, at 25% base length of fold	2.2	1.9	2.0	2.6
Fold depth, at 25% of its base length	2.3	2.3	2.5	3.9
Tail width, at mid-base length of fold	1.3	1.1	1.1	1.5
Tail depth, at mid-base length of fold	1.5	1.6	1.8	2.0
Fold depth, at its mid-base	2.1	1.8	2.0	5.1
Tail width, at 75% base length of fold	0.8	0.8	0.9	1.2
Tail depth, at 75% base length of fold	1.2	1.2	1.3	1.5
Fold depth, at 75% of its base length	1.2	1.1	1.3	4.3
Tail width, insertion of fold	0.7	0.6	0.7	1.0

Table 1. cont'd.

		Paratypes (n=2)		MTUF
	Holotype	Min.	Max.	specimen
Tail depth, insertion of fold	0.8	0.8	0.8	1.1
Fold origin-sting origin, length	2.3	2.0	4.1	5.4
Sting length	–	–	–	28.6
Snout to origin of cloaca	77.3	77.6	78.7	78.2
Cloaca origin to sting	77.0	80.0	84.0	78.1
Cloaca origin to tail tip	257.3	240.9	274.2	324.8
Cloaca length	6.5	6.7	6.7	6.0
Clasper, postcloaca length	25.9	–	26.3	13.0
Clasper, length from pelvic axil	13.5	–	14.4	4.7

almost straight posteriorly; posterior margin straight to weakly convex; apex angular; free rear tip broadly rounded; length moderate, 21.6% (22.2–24.1%) DW, subequal to width across fin base in holotype and male paratype (i.e. 0.99, 1.00), 1.09 times longer in female paratype. Tail moderately elongate, postcloacal tail 3.33 (3.06–3.53) times precloacal length; base depressed, width 1.81 (1.78–1.81) times height, weakly convex above and below, narrowly rounded laterally; tapering gently and evenly to origin of sting, width 1.29 (1.29–1.33) times height at fold origin; strongly tapering, naked post-sting groove on dorsal surface, tail slightly depressed at end of groove; at mid-fold moderately compressed, oval, width 0.86 (0.61–0.67) times height; at end of fold weakly compressed, width 0.92 (0.83–0.88) times height; finely filamentous, becoming depressed towards tail apex; no folds present along lateral margin of anterior pre-sting tail. Ventral cutaneous fold very slender, length 0.91 (0.90–0.91) in disc width, 2.34 (2.19–2.46) in postcloacal tail; origin 2.3% (2.0–4.1%) DW before sting origin; depth at quarter length 1.05 (1.22–1.26), at mid length 1.43 (0.99–1.24), at three quarter 0.98 (0.86–1.00) times tail height; margin of terminal quarter of fold not strongly indented in holotype, not terminating abruptly, continuing much more than orbit diameter along tail as a low, barely detectable ridge; distance from cloaca to sting origin 1.00 (0.94–0.97) in precloacal length; post-fold tail length 1.55 (1.29–2.19) in fold length, 3.62 (3.18–4.18) in tail length. No U-shaped clusters of sensory pores submarginal on posterior disc. Lateral line on ventral surface indistinct.

Snout moderately elongate, acute at apex with small, triangular apical lobe; angle 117 in paratype CSIRO H 7110–01; acutely subtriangular when viewed laterally, becoming strongly depressed towards apex, preoral snout length 2.31 (2.23–2.26) times mouth width, 2.41 (2.44–2.44) times internarial distance, 0.92 (0.93–1.02) times distance between first gill slits; direct preorbital snout length 1.92 (1.96–1.98) times interorbital length; snout to maximum disc width 2.61 (2.50–2.54) times in DW; interorbital space very broad, weakly convex to flat; eyes small, dorsolateral, elevated and protruding slightly, ventral margin partly covered by thin, fleshy skin fold; orbit weakly fused into head, obvious, diameter 1.40 (1.49–1.59) in spiracle length, eye diameter 2.62 (2.50–2.70) in spiracle length; inter-eye distance 6.29 (5.84–6.09) times eye diameter length. Spiracles suboval, greatly enlarged, opening dorsolateral. Nostril slit-like, curved, directed posterolaterally; anterior margin fleshy; anterior nasal fold internal, thin, membranous; posterior lobe more greatly expanded and fleshy than anterior lobe, partly concealed beneath nasal curtain; oronasal groove present; internasal distance 1.93 (1.85–1.87) in prenasal length, 2.18 (2.15) times nostril length. Nasal curtain distinctly bilobed, relatively elongate, long, flat, with no obvious longitudinal medial groove, almost smooth, width 1.76 (1.76–1.85) times length, posterolateral apex recessible within lateral margin of oronasal groove; lateral margin slightly convex distally, smooth edged; posterior margin very finely fringed (obscure), strongly concave, following contour of lower jaw, overlaying symphysis of lower jaw when mouth closed. Jaws strongly asymmetric. Upper jaw very strongly arched, symphysial part of jaw projecting posteroventrally, forming a perpendicular angle with anterior lateral teeth (jaw not dissected but appears to be typical of other members of the genus). Lower jaw interlocking upper jaw when mouth closed; mouth not protrusible; skin on chin not especially fleshy, weakly papillose to almost smooth; oral papillae and tooth morphology not examined.

Gill openings strongly S-shaped, forming a unfringed lobe; length of first gill slit 1.36 (1.18–1.20) times length of fifth gill slit, 2.68 (2.81– 2.88) times in mouth width; distance between first gill slits 2.62 (2.40–2.62) times internasal distance, 0.47 (0.43–0.46) times ventral head length; distance between fifth gill slits 1.75 (1.64–1.68) times internasal distance, 0.31 (0.30) times ventral head length.

Dorsal disc mostly covered in denticles; main denticle band extending to disc margin anteriorly, to about distance equivalent to preorbital snout length from pectoral-fin apex, posterior part of disc with minute, widely spaced denticles; narrow naked strip extending anteriorly from pectoral-fin insertion; pelvic fins and claspers naked; rim of eye and posterior extremity merging into spiracle naked; denticles present on distal half of posterior wall of spiracle. Denticle band with 2 well-separated pearl thorns; thorns very similar in size, elevated above disc, separated by slightly less than their length, their dorsal margin strongly convex when view laterally; denticles on mid-disc and interorbital space distinctly larger than those laterally, also slightly more widely spaced than those laterally; denticles in lateral part of band similar in size, not becoming progressively smaller towards lateral margin of band; lateral margin of band with longitudinal denticle rows often separated by very narrow naked strips; denticles covering entire snout, less densely arranged than those on mid-disc, much larger than those along lateral margin but much smaller than those of mid-disc; denticle band merging with tail at pectoral-fin insertion, not truncate or laterally expanded. Tail with single row of small, variably spaced, pungent thorns; thorns short-based, semi-upright, short lanceolate, commencing above pelvic-fin insertion, decreasing in size posteriorly, merging in size with tail denticles before sting; entire dorsal and dorsolateral surfaces of tail covered with small denticles at tail base, tail band covering more than three quarters of dorsal surface of most of tail before skin-fold origin (but edges naked when viewed dorsally); denticle band descending ventrally just posterior to fold origin to cover most of lateral surface of tail; ventralmost portion adjacent tail fold naked; skin fold naked, smooth or with fine posteroventrally directed striae. Single irregular series of keel-like denticles along dorsal midline of tail behind sting; denticles sparse, elevated, upright, compressed, subtriangular, their height slightly taller than denticles of snout; denticles probably deciduous, midline of tail partly naked with scars demarcating position of lost denticles; main denticles of posterior tail seed-shaped, elongated longitudinally. Denticles on mid-disc stellate; crowns flat topped, barely raised, not significantly narrower than their bases. Denticles on anterior half of snout stellate in appearance, upright, widely spaced; crowns elevated, broad, with 3–5 obvious cusps, usually directed posterodorsally; ventral surface of disc, and tail forward of ventral fold, naked. Male holotype with stinging spine broken. Clasper strongly conical, slightly depressed, robust basally and tapering distally to a blunt point.

Figure 3. *Pastinachus stellurostris* sp. nov., female paratype (NCIP 6338, 413 mm DW, preserved): dorsal head.

Figure 4. Oronasal region of *Pastinachus stellurostris* sp. nov., adult male paratype (CSIRO H 7110–01, 415 mm DW, preserved).

Meristic data for paratype CSIRO H 7110–01 (values for non-type from Thailand, MTUF P 30003 in parentheses): total pectoral radials 117 (about 114); propterygials 48–49 (about 50), mesopterygials 17–18 (about 14) and metapterygials 51 (about 50). Total pelvic radials 24. Total vertebral segments (centra, exc. synarcual) 161 (159); postsynarcual monospondylous centra 36 (36); diplospondylous centra about 125 (123).

COLORATION.— Holotype, when fresh: Uniformly dark brown dorsally, with a faint greenish tinge; suprascapular thorns pearly white; median thorns along tail slightly paler than rest of tail. Ventral surface usually with pinkish tinges from fresh blood; margin of disc and pelvic fins narrowly dusky; teeth orange brown, mouth

white; tail base whitish, greyish brown toward sting; ventral skin fold pale brownish blue, darkest distally. First specimen collected (KA 306, adult male) had a uniform, yellowish brown dorsal disc with a paler post-sting tail. In preservative (adult male paratype, CSIRO H 7110–01): Uniformly brown dorsally, slightly paler near pectoral apices and on naked part of tail beside denticle band; ventral surface mostly white, darker greyish black areas along edge of disc, more broadly on pelvic-fin margins, around cloaca, and at tip of clasper; ventral tail white with some dusky areas; ventral half of tail beside skin fold whitish, fold whitish basally with outer part bluish brown.

SIZE.— Attains at least 428 mm DW (adult male); two other adult males, 422 and 415 mm DW.

ETYMOLOGY.— Derived by combination of the Greek *stella* (starry) and Latin *rostrum* (snout) in allusion to the characteristic star-shaped denticles on the snout. Vernacular: Starrynose Stingray.

DISTRIBUTION.— Known from West Kalimantan in the vicinity of the Kapuas River estuary and near Pemangkat. Probably prefers shallow, fresh or brackish water habitats. Possibly misidentified locally as other species of *Pastinachus* and may be more widely distributed in parts of Borneo, and even Sumatra, where the habitat is suitable. A juvenile male (MTUF P 30003), collected about 60 km upstream from the mouth of the Bang Pakong River in Thailand, may represent the first record of this species outside Borneo. More specimens are needed from continental Asia to resolve this issue.

COMPARISONS.— *Pastinachus stellurostris* and *P. solocirostris* differ from other members of the genus in having an angular snout covered to its tip by enlarged spiny denticles (Fig. 7), and a relatively long slender ventral skin fold. *Pastinachus stellurostris* differs from *P. solocirostris* in squamation and also appears to differ in several morphometric characters. Along with *P. gracilicaudus*, they both have enlarged pearl-shaped suprascapular thorns, however, thorns along the midline of the tail are found in *P. stellurostris* and no other cowtail ray. Denticles at the snout tip of *P. stellurostris* are stellate (Fig. 7a) whereas they are simpler and more elongate to lanceolate in *P. solocirostris* (Fig. 7b). The eye of *P. stellurostris* also protrudes more than that of *P. solocirostris*. The following standard ratios are relatively smaller in *P. stellurostris*: head length 43.7–45.1% DW (47.1–50.9% DW); snout 20.7–22.4% DW (22.4–28.0% DW); preoral 19.0–19.5% DW (21.4–25.0% DW); prenasal 14.7–15.3% DW (16.6–19.2% DW); orbit and spiracle length 8.7–9.8% DW (10.4–11.0% DW); and nasal curtain length 5.6–6.0% DW (6.7–7.9% DW). Several width-related ratios are smaller in *P. stellurostris*: inter-eye width 15.7–16.6% DW (16.9–20.2% DW); interspiracular width 16.5–17.6% DW (17.5–19.8% DW); nasal curtain width 10.1–10.5% DW (11.4–13.9% DW); internasal width 7.9–8.0% DW (8.6–11.1% DW); and distance between 1st gill slits 19.0–20.8% DW (20.4–25.2% DW). In addition, the eye of *P. stellurostris* appears to be smaller (diameter 2.5–2.8% DW vs. 2.8–4.0% DW); distances from the snout to the point of maximum width of the disc (38.3–40.0% DW vs. 42.7–52.0% DW) and cloaca origin to sting (77.0–84.0% DW vs. 85.2–93.9% DW) shorter; and the post-sting tail is marginally more compressed (tail width at mid-base length of ventral fold 1.1–1.3% DW vs. 1.2–1.5% DW), with a much more slender ventral skin fold (depth at its mid-base 1.8–2.1% DW vs. 2.7–3.7% DW; depth at posterior quarter of its base length 1.2–1.3% DW vs. 2.2–4.0% DW). The pelvic-fin base is relatively broader in *P. stellurostris* (21.6–22.4% DW vs. 15.8–21.2% DW).

Figure 5. Mouth of *Pastinachus stellurostris* sp. nov., female paratype (NCIP 6338, 413 mm DW, preserved).

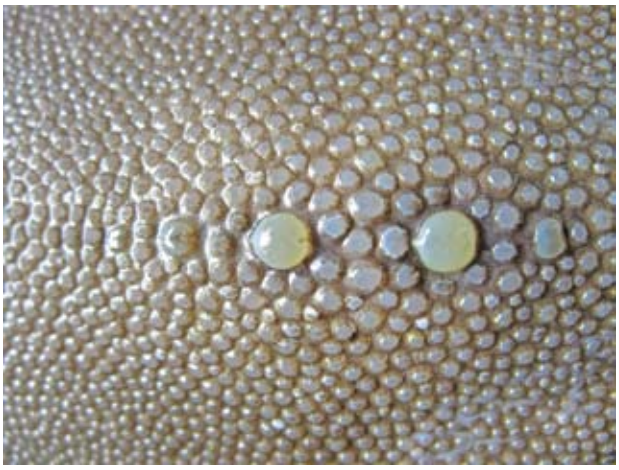

Figure 6. Squamation in the mid-scapular region of *Pastinachus stellurostris* sp. nov., female paratype (NCIP 6338, 413 mm DW, preserved).

REMARKS.— Molecular data also confirmed that *Pastinachus stellurostris* and *P. solocirostris* are not conspecific. DNA sequence data were determined for the mitochondrial protein coding gene NADH2 for 13 specimens of *Pastinachus atrus*, 9 of *P. gracilicaudus*, 11 of *P. solocirostris* and one of *P. stellurostris* (GN 4600); a specimen of *Dasyatis zugei* was used as an outgroup. The sequence data were aligned and subjected to Maximum Likelihood Analysis using a General Time Reversible model with allowance for among-site rate variation and invariant sites. The resulting topology revealed 4 distinct clades representing 4 valid species of *Pastinachus* (Fig. 10). Interestingly, the variation within *P. atrus* from geographically disparate localities (Australia, Madagascar, Philippines, Indonesia and Malaysia) was comparable to levels observed within *P. solocirostris* or *P. gracilicaudus* taken from around the Island of Borneo.

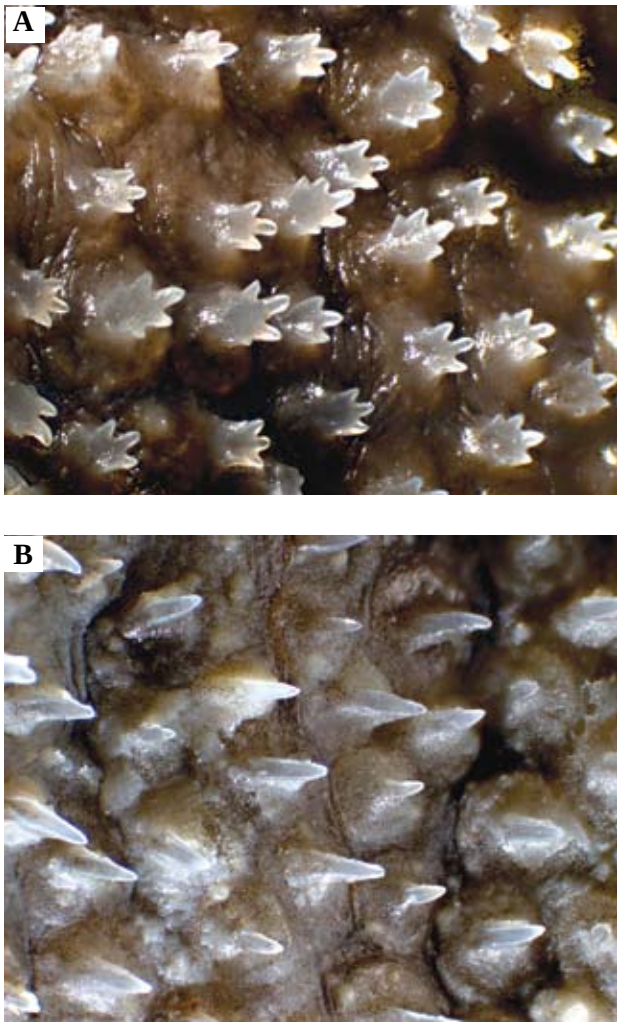

Figure 7. Denticles of the snout tip of: A. *Pastinachus stellurostris* sp. nov., adult male paratype (CSIRO H 7110–01, 415 mm DW, preserved); B. *Pastinachus solocirostris*, CSIRO H 6219–01, female paratype 416 mm DW, preserved).

Figure 8. Lateral view of the tail of *Pastinachus stellurostris* sp. nov., adult male paratype (CSIRO H 7110–01, 415 mm DW, preserved), at the mid region of the ventral cutaneous fold.

The distribution of *P. stellurostris* in the region is unclear. A 235 mm immature male, collected in Bang Pakong River, Thailand (MTUF P 30003), is similar in morphology to the larger, type specimens of *P. stellurostris* from Borneo, most of which are adults. This specimen also possesses stellate denticles at the snout tip, a row of small thorns along the midline of the anterior tail, a long and very low skin fold, and large pearl-shaped thorns on the suprascapular region. Morphometric and meristic details are also similar to the types of *P. stellurostris*; the main differences being a markedly broader intereye (17.5% vs. 15.7–16.6% DW), interspiracular (18.7% vs. 16.5–17.6% DW), internasal distance (8.6% vs. 7.9–8.0% DW) and distance between the first gill slits (21.9% vs. 19.0–20.8% DW), longer pelvic fin (26.9% vs. 21.6–24.1% DW) but narrower base width (17.3% vs. 21.6–22.4% DW), much longer ventral fold length (1.23 vs. 1.10–1.12 times DW), and a broader posterior tail (its width 4.8% vs. 4.0–4.1% DW and depth 3.7% vs. 3.0–3.2% DW at origin of ventral fold) in the Thai specimen. The main difference between these forms is in the ventral disc and tail coloration; in the Thai specimen, the disc is largely dark brown with some pale areas (rather than almost entirely white) and the tail is uniformly dark brown (vs. almost entirely white with faint dusky areas). Ventral coloration can be an important species-level character in dasyatids so, for this reason, this specimen was omitted from the type series. More material from continental Asia is needed to assess possible conspecificity of these populations.

Comparative material referred to in this paper: *Pastinachus solocirostris*: CSIRO H 6219–01 (paratype), 416 mm DW, female, Sematan Fish Market, Sarawak, Malaysia, 15 May 2003.

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Figure 9. *Pastinachus* cf. *stellurostris*, immature male (MTUF P 30003, 235 mm DW, preserved), from Thailand: A. dorsal surface; B. ventral surface.

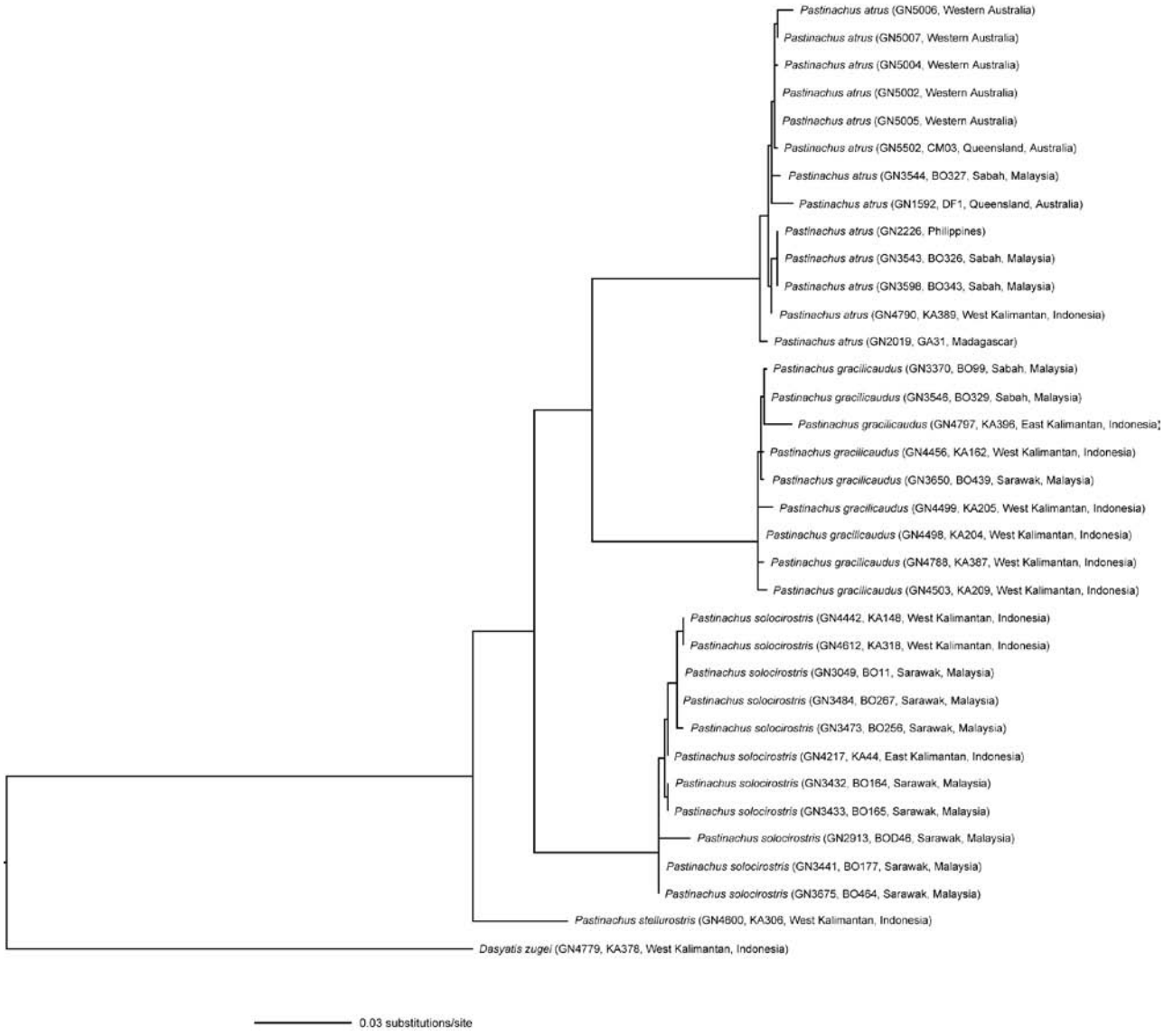

Figure 10. Maximum Likelihood Tree resulting from analysis of NADH2 DNA sequence data. Log Likelihood score for this tree was 3308.707 using a General Time Reversible model with accommodation for among site rate variation and invariant sites.

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Clarification of *Aetobatus ocellatus* (Kuhl, 1823) as a valid species, and a comparison with *Aetobatus narinari* (Euphrasen, 1790) (Rajiformes: Myliobatidae)

William T. White[1], Peter R. Last[1], Gavin J.P. Naylor[2], Kirsten Jensen[3] & Janine N. Caira[4]

[1] CSIRO Marine & Atmospheric Research, Wealth from Oceans Flagship, GPO Box 1538, Hobart, TAS, 7001, AUSTRALIA
[2] Florida State University, School of Computational Science/Department of Biological Science, Tallahassee, FL 32304, USA
[3] Organismal Biology, The University of Kansas, Lawrence, Kansas 66045, USA
[4] Department of Ecology and Evolutionary Biology, University of Connecticut, 75N Eagleville Road, U–43, Storrs, CT, USA

ABSTRACT.— *Aetobatus narinari* is generally considered to have a circumglobal distribution but some have suggested that it consists of more than one cryptic species. Recent molecular studies have provided evidence of a species complex, with an Indo–West/Central Pacific clade and a Western Atlantic clade. This paper investigates the nomenclature of the Indo–West Pacific species and provides a redescription of *Aetobatus ocellatus* (Kuhl, 1823). *Aetobatus ocellatus* is very similar morphologically to *Aetobatus narinari* but differs in having a slightly longer tail and a different dorsal coloration. A major taxonomic revision of the *A. narinari* complex is required to determine the number of species present, their distributional ranges and effective field characters. The conservation status of members of this complex needs to be evaluated.

Key words: *Aetobatus ocellatus* – *Aetobatus narinari* – Indo–West Pacific – redescription – eagle rays

PDF contact: william.white@csiro.au

INTRODUCTION

The family Myliobatidae, eagle rays (Chondrichthyes: Rajiformes), a group of medium to large rays with wing-like pectoral fins, is comprised of four genera. The genus *Myliobatis* has the largest number of valid nominal species (12) compared with *Aetobatus* (at least 3), *Aetomylaeus* (4) and *Pteromylaeus* (2). Members of the genus *Aetobatus* differ from the other genera in having a deeply notched nasal curtain, the upper and lower teeth in a single row at all growth stages, and the lower jaw with chevron-shaped teeth (Capapé & Quignard, 1975; Compagno & Last, 1999). The supraspecific taxon *Aetobatus* was designated by Blainville (1816) as a subgenus for *Raja aquila*; the type species for the genus *Aetobatus* was subsequently designated to be *Raja narinari* by Müller & Henle (1841).

Two nominal species, *A. narinari* and *A. flagellum* (Bloch & Schneider, 1801), within this genus are generally considered valid, with *A. guttata* (Shaw, 1804) and *A. ocellatus* (Kuhl, 1823) listed as questionable species by some authors. *Aetobatus narinari* was described by Euphrasen (1790), as *Raja narinari*, and in his description he clearly refers to the 'Narinari brasiliensibus' of Willughby (1686) based on a specimen from Brazil, as well as a specimen he collected from St Barthelemy in the West Indies. Thus, both of these Western Atlantic locations are considered type localities for this species (Eschmeyer, 2009). Although some authors placed *A. flagellum* in the synonymy of *A. narinari* (e.g. Fowler, 1941; Dor, 1984), this species is a smaller, valid member of the genus *Aetobatus* (Compagno & Last, 1999; White *et al*., 2006).

Aetobatus narinari has historically been considered to have a circumtropical distribution, but some studies have suggested that it may consist of a species complex (e.g. Jensen & Caira, 1998; Compagno & Last, 1999; Compagno *et al*., 2005; Marie & Justine, 2005; Last & Stevens, 2009). A recent molecular study by Richards *et al.* (2009) assessed the validity of *A. narinari* as a single, widespread species using mitochondrial and nuclear sequence data from specimens collected in the Western, Central and Eastern Pacific and the Western Atlantic Oceans. Their findings provided strong evidence that this species is indeed a complex of at least 2 or 3 species, with the Western/Central Pacific lineage clearly distinct from the Western Atlantic and Eastern Pacific. This then raises the issue of what species name is available for the Indo–

West/Central Pacific species, and how it differs from the other species in this complex.

In the Indo–West/Central Pacific region, the *A. narinari* complex has a complicated nomenclatural history that needs to be critically examined. Two species names were proposed by Forsskål (1775) for *A. narinari*-like species from the Red Sea. The first of these, *Raja mula*, is considered available (Fricke, 2008), but since it hasn't been used as a valid name since 1899, it should be considered *nomen oblitum*. The second, *Raja tajara hörraeka*, is unavailable as it is not binominal because alternative Arabic vernacular names were used (Eschmeyer, 2009). Russell (1803) provided a short, but adequate, description and figure of an *Aetobatus* from Coromandel in India, but as with the other species in his substantial publication, he assigned only a vernacular name (Eel tenkee) which is non-binominal and cannot be considered an available name (ICZN Art. 11.4). In 1804, Shaw described the Guttated Ray *Raja guttata*, in a composite description based on records from India (based on Russell, 1803), Madagascar (based on records from Commerson) and Brazil (Marcgrave, 1648). However, since no types were designated and it is now known to consist of multiple species, use of this species name does not support nomenclatural stability. Furthermore, the name *Raja guttata* Shaw, 1804 is objectively invalid as it is a primary homonym of *Raja guttata* Bloch & Schneider, 1801 and thus must not be used (R. Fricke, pers. comm.).

In 1823, Kuhl provided a brief description of a new eagle ray, *Myliobatus ocellatus*, from Java (Indonesia) and reported that it agrees with Russell's (1803) illustration of 'Eel tenkee' from India, but no types were designated. *Aetobatus ocellatus* has been referred to as a valid taxon by a number of authors (Garman, 1913; Fowler, 1941; Talwar & Kacker, 1984; Talwar & Jhingran, 1992; Goren & Dor, 1994; Mould, 1994; Froese *et al*., 1996; Kapoor *et al*., 2002; Sujatha, 2002; Bonfil & Abdallah, 2004; Eschmeyer, 2009; Richards *et al*., 2009). Thus, *Aetobatus ocellatus* (Kuhl, 1823) is the first available suitable name for the Indo–West/Central Pacific member of the *A. narinari* complex, with Java as the type locality. A number of species have been described since Kuhl's description of *A. ocellatus* from the Indo–West/Central Pacific that are considered conspecific with *A. narinari*. These include *Raia quinqueaculeata* Quoy & Gaimard, 1824, *Myliobatis eeltenkee* Rüppell, 1837, *M. macroptera* McLelland, 1841, *Raja edentula* Forster *in* Lichtenstein, 1844, *Goniobatis meleagris* Agassiz, 1858, and *Myliobatis punctatus* Miklukho-Maclay & Macleay, 1886. These should be considered junior synonyms of *Aetobatus ocellatus*.

In other regions of the world, the nomenclatural history of the *A. narinari* group is far more stable. In the Eastern Pacific, Gill (1865) described *Aetobatis laticeps* from off California, and in the Eastern Atlantic, Duméril (1861) described *Aetobatis latirostris* from off Gabon, West Africa. Both of these species have since been considered junior synonyms of *Aetobatus narinari*. There are no junior synonyms of *A. narinari* in the Western Atlantic.

The present study provides a redescription of *Aetobatus ocellatus* as a valid species and designates a neotype for the species. Comparisons are made with *Aetobatus narinari* from the Western Atlantic.

Since the turn of the 20th Century (e.g. Shipley, 1900), the metazoan parasites of "*Aetobatus narinari*" have been the focus of numerous studies. Although in many cases, the notion that the "spotted eagleray" may actually consist of a complex of species has gone largely unnoticed by parasitologists (e.g. Shipley & Hornell, 1906; Linton, 1916; Brooks & Mayes, 1980; Marques *et al.*, 1997), this has not always been the case. For example, Jensen & Caira (1998) reported differences in the tapeworm faunas of host specimens identified as "*Aetobatus narinari*" collected from the Gulf of California, Gulf of Thailand and Timor Sea in Australia that might be indicative of the lack of conspecificity of spotted eagle rays among these localities. More recently, Marie & Justine (2005) reported that, of the 7 species of monocotylid monogeneans reported from spotted eagle rays, 5 species were known only from spotted eagle rays taken from localities in the Indo–Pacific, and not from those taken from the Atlantic Ocean. Marie & Justine (2006) explored this notion more formally, focusing specifically on a species of the monocotylid monogenean genus *Thaumatocotyle* that appears to parasitise spotted eagle rays in the Atlantic and Pacific Oceans. In fact, cognizant of the potential existence of a complex of host species, Marie & Justine (2005, 2006) referred to the host of their worms as *Aetobatus* cf. *narinari*.

The primary objective of the parasitic treatments provided in this paper is to place the previous records of metazoan parasites of spotted eagle rays (*A. narinari* complex) into the context of the taxonomic determinations for this ray complex proposed here. Thus, the names attributed to host individuals for the parasite records presented here have been modified, based on the localities from which the stingray hosts were collected, to reflect the eagle ray taxonomy proposed here. Clearly these treatments would benefit greatly from further investigation.

METHODS

Morphometric characters were established for eagle rays and are defined in Table 1. A total of 65 measurements, expressed as proportional measurements of disc width (DW), were taken for the neotype (MZB 18225) of *Aetobatus ocellatus* and 11 other specimens (CSIRO H 2490–01, CSIRO H 4426–19, CSIRO H 6131–02, IPMB 38.01.08, IPPS BO296, IPPS HBO2, RMNH 33021, RMNH unregistered, SMEC 75, SMEC 76 and SMEC

Table 1. Definition of the morphometric characters taken for myliobatid rays.

Morphometric character	Methodology
Disc width	Direct distance between pectoral-fin apices
Total length	Direct distance from snout tip to tip of tail (when undamaged)
Pre-dorsal length	Direct distance from snout tip to origin of dorsal fin
Disc length	Direct distance from snout tip to pectoral-fin free rear tip
Snout to pectoral-fin insertion	Direct distance from snout tip to insertion of pectoral fin (taken in dorsal position)
Disc thickness	Greatest thickness of body (usually under scapular region)
Snout to pectoral-fin origin	Direct distance from snout tip to origin of pectoral fin (use thumb to feel location of origin)
Posterior orbit to pectoral-fin insertion	Direct distance from the posterior edge of orbit (not eye) to insertion of pectoral fin
Snout to maximum width (horiz.)	Horizontal distance from snout tip to level of greatest width of body (run a line between pectoral-fin apices and place a pin at this level on the dorsal midline, then measure from snout tip to pin)
Pectoral-fin anterior margin	Distance from origin of pectoral fin to its apex
Pectoral-fin posterior margin	Distance from apex of pectoral fin to its free rear tip (if rounded use point of greatest angle)
Pectoral-fin base length	Distance from origin of pectoral fin to its insertion (taken in dorsal position)
Pectoral-fin inner margin	Distance from insertion of pectoral fin (taken in dorsal position) to its free rear tip (if rounded use point of greatest angle)
Head length (ventral)	Direct distance from inner edge of fifth gill slit to snout tip
Preorbital length	Direct distance from anterior edge of orbit to snout tip
Preorbital length (horiz.)	Horizontal distance from anterior edges of orbits to snout tip
Head width at pectoral-fin origins	Width of head at pectoral-fin origins (use thumb to feel location of origin)
Head height at pectoral-fin origins	Vertical height of head at pectoral-fin origins (use thumb to feel location of origin)
Head width at mid-eye	Width of head at level of mid-eye
Head height at mid-eye	Vertical height of head at level of mid-eye
Interorbital width	Distance between inner-most soft margins of each orbit (press calipers in against cranium on either side at mid-orbits)
Interspiracular width	Distance between inner-most margins of each spiracle
Spiracle length (longest)	Greatest diameter of the spiracle
Spiracle width (narrowest)	Diameter of the spiracle perpendicular to above measurement
Orbit diameter	Greatest diameter of the orbit (not exposed eye)
Eye diameter	Greatest diameter of the eye (not including outer orbit structure)
Orbit and spiracle length	Distance from anterior margin of orbit to posteriormost edge of the spiracle aperture
Preoral length	Direct distance from snout tip to soft anterior edge of lower jaw (not to tooth plates if extended anteriorly)
Prenasal length	Direct distance from snout tip to anterior margin of left nostril
Prenasal length (horiz.)	Horizontal distance from snout tip to anterior margins of nostrils
Rostral lobe width	Width of rostral lobe (taken below mideye)
Rostral lobe length	Direct distance from snout tip to posterior edge of rostral lobe (if exact location of posterior edge not clear use point of greatest angle)
Mouth width	Width of exposed part of mouth
Internarial width (external)	Shortest distance between incurrent nasal apertures
Nasal curtain length	Horizontal measurement from anteriormost margin of nostril to posterior margin of nasal curtain
Nasal curtain width	Greatest width of nasal curtain

Table 1. cont'd.

Morphometric character	Methodology
Nostril length (internal)	Greatest diameter of nostril (taken by elevating left side of nasal flap to reveal nostril)
Width of first gill slit	Greatest width of first gill slit
Width of third gill slit	Greatest width of third gill slit
Width of fifth gill slit	Greatest width of fifth gill slit
Distance between first gill slits	Shortest distance between first gill openings
Distance between fifth gill slits	Shortest distance between fifth gill openings
Tail at axil of pelvic fins (width)	Width of tail at pelvic-fin insertion
Tail at axil of pelvic fins (height)	Height of tail at pelvic-fin insertion
Tail at origin of stinging spine(s) (width)	Width of tail at origin of stinging spine (when >1 stings present base on origin of first sting)
Tail at origin of stinging spine(s) (height)	Height of tail at origin of stinging spine (when >1 stings present base on origin of first sting)
Pectoral-fin insertion to spine origin (horiz.)	Horizontal distance from pectoral-fin insertions to origin of stinging spine
Length of first stinging spine	Length of stinging spine from its exposed origin to its tip (taken in dorsal view)
Length of second stinging spine	Length of second stinging spine, when present, from its exposed origin to its tip (origin usually located beneath first sting)
Pectoral-fin insertion to dorsal-fin origin (horiz.)	Horizontal distance from pectoral-fin insertions to origin of dorsal fin
Dorsal-fin length	Direct distance from origin of dorsal fin to its free rear tip
Dorsal-fin anterior margin	Direct distance from origin of dorsal fin to its apex
Dorsal-fin height	Vertical height of fin from its base to its apex
Dorsal-fin posterior margin	Direct distance from apex of dorsal fin to its free rear tip
Dorsal-fin inner margin	Direct distance from insertion of dorsal fin to its free rear tip
Snout to anterior cloaca	Direct distance from snout tip to the anteriormost edge of the cloaca
Cloaca anterior to tail tip	Direct distance from the anteriormost edge of the cloaca to the tail tip (when undamaged)
Cloaca anterior to stinging spine	Horizontal distance from the anteriormost edge of the cloaca to origin of the stinging spine(s)
Width across pelvic fin bases	Direct distance between pelvic-fin origins (based on visible origins and not embedded, cartilaginous structures)
Greatest span of pelvic fins	Greatest span of pelvic fins when placed in natural position (not stretched)
Pelvic-fin length	Distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to posteriormost point of fin
Pelvic-fin anterior margin	Direct distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to its apex (use point of greatest angle when broadly rounded)
Pelvic-fin base	Direct distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to its insertion
Pelvic-fin posterior margin	Direct distance from apex of pelvic fin to its free rear tip (use point of greatest angle when broadly rounded)
Pelvic-fin inner margin	Direct distance from insertion of pelvic fin to its origin (based on visible origins and not embedded, cartilaginous structures)

244). For comparison, 5 specimens of *A. narinari* from the Western Atlantic were measured in full. Meristics were obtained from radiographs of the neotype (MZB 18225) and 3 other specimens of *Aetobatus ocellatus* (CSIRO H 2490–01, CSIRO H 4426–19, CSIRO H 6131–02). Counts generally follow Last & White (2008) for dasyatids, with some minor modifications: the first enlarged anterior element of the pelvic fin (with at least 4 and up to 6 distal segments fused at their bases) is counted as one; first synarcual centra are included in vertebral counts as there are no denticles to obscure centra; pre-dorsal diplospondylous counts are used rather than pre-sting counts; intermediate pectoral-fin radial elements were assigned to a pterygial unit based on the relative level of overlap with each of the adjacent units; and distal propterygial and metapterygial elements were considered to form part of the main skeleton and were not incorporated into counts; the notochord of the tail was excluded from counts. Only juvenile specimens were radiographed and some parts were poorly calcified. Pectoral and pelvic radial counts indicated by an asterix (*) are minimum counts as additional radials not evident on radiograph may be present. A question mark indicates that the count was not possible due to poor calcification or inadequate exposure.

Muscle tissue samples were taken from specimens collected in the field and stored in either 95% alcohol or DMSO until processed in the laboratory. Total DNA was extracted from the tissue samples using High Pure PCR Template Preparation Kit (Roche Diagnostics). Extracted total DNA was stored at –20° C. Sub-sets of the extracted template were diluted to 1/10 of original strength and stored for subsequent use in PCR reactions. Samples were PCR amplified using Hot Start Taq (Promega) using primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (Naylor *et al*., 2005). These primers are designed to bind to the ASN and ILE tRNA regions flanking the NADH2 gene in the mitochondrial genome of elasmobranchs. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of T.aq, PCR buffer, 2.5 mM, MgCL2, 1.0 mM of DNTPs, and 1.0 mM of each primer. The reaction cocktail was denaturised at 94˚C for 3 minutes, after which it was subjected to 35 cycles of 94°C /30s, 48°C /30s and 72°C /90s followed by an indefinite hold in the thermal cycler at 4°C.

A sample of the completed PCR reaction was run on 1% agarose gels, stained, visualised and photographed under UV light to assess the success of PCR amplification. Samples with successful amplification products were purified using purification plates (Millipore, MA) attached to a vacuum manifold. The purified PCR products were quantified and diluted to between 30–100 ng/µL and subsequently sent to SeqWright (Houston, TX) for sequencing. The software packages Phred and Phrap were used to read sequence traces, assign quality values, make base calls and produce output files for subsequent alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment.

The aligned nucleotide sequences were subjected to Phylogenetic analysis using PAUP* (v4.0b106). The data were subjected to Neighbour joining based on K2P Distance, Parsimony and Maximum Likelihood analysis using parameter optimised models that best fit the data. The topologies across all methods were consistent with each other.

Specimens are referred to by the following prefixes for their registration numbers: BMNH, British Museum of Natural History, London; CSIRO, Australian National Fish Collection, Hobart; IPMB, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia; IPPS, Institut Penyelidikan Perikanan Sarawak, Kuching, Sarawak; MNHN, Muséum national d'Histoire naturelle, Paris; MZB, Museum Zoologicum Bogoriense, Jakarta; RMNH, Rikjsmuseum van Natuurlkjke Histoire, Leiden; SMEC, Zoology Department of the Sabah State Museum, Kota Kinabalu, Malaysia. In the molecular trees, field codes (prefixed by AU, BJ, BO, BOD, CM, FY, HBO, JDD, NT or KA) are provided for samples collected by three of us (JC, KJ, GN), and data and images for these specimens are available at http://tapeworms.uconn.edu.

SYSTEMATIC ACCOUNT

Genus *Aetobatus* Blainville, 1816: 122 (Type species: *Raja narinari* Euphrasen)

Leiobatus Klein, 1775: 316 (not valid: does not conform to binominal nomenclature)
Leiobatis Walbaum (ex Klein), 1792: 581 (not available: work rejected for nomenclatural purposes)
Aetobatis Blainville, 1825: 38 (incorrect spelling of *Aetobatus*)
Aetobates Richardson, 1846: 198 (incorrect spelling of *Aetobatus*)
Stoasodon Cantor, 1849: 1416 (Type species: *Raja narinari* Euphrasen, monotypic)
Goniobatis Agassiz, 1858: 385 (Type species: *Raja flagellum* Bloch & Schneider, monotypic)

SPECIES.— *Aetobatus* includes at least 3 nominal species, *A. flagellum* (Bloch & Schneider), *A. narinari* (Euphrasen, 1790), and *A. ocellatus* (Kuhl, 1823). *Aetobatus laticeps* (Gill, 1865) from the Eastern Pacific is probably also valid but no specimens were examined during this study. *Aetobatus latirostris* (Duméril, 1861) from the Eastern Atlantic, also currently considered a synonym of *A. narinari*, is questionable and requires further investigation. At least one apparently undescribed species also occurs in the North-west Pacific.

Aetobatus ocellatus (Kuhl, 1823)

Figs 1–6, Table 2

Raja mula Forsskål, 1775: ix (Jeddah, Red Sea).
Raja tajara Forsskål, 1775: ix (Jeddah, Red Sea).
Raja narinari (non Euphrasen): Bloch & Schneider, 1801: 361 (Tahiti).
Eel tenkee Russell, 1803: 5, pl. 8 (Coromandel, India). Binominal system of naming not used thus not valid.
Raja guttata (non Bloch & Schneider): Shaw, 1804 (type locality: Madagascar, Coromandel, Brazil). Objectively invalid.
Myliobatus ocellatus Kuhl, 1823 (type locality: Java, Indonesia).
Raia quinqueaculeata Quoy & Gaimard, 1824: 200, pl. 43 (type locality: Guam).
Myliobatis narinari (non Euphrasen): [Bennett, 1830]: 694 (Sumatra).
Myliobatis eeltenkee Rüppell, 1837: 70, pl. 19, fig. 3 (type locality: Jeddah in Saudi Arabia; Massawa in Red Sea).
Aetobatis indica: Swainson, 1839: 321 (based on Russell, 1803: Coromandel, India).
Myliobatis macroptera McLelland, 1841: 60, pl. 2, fig. 1 (type locality: Bengal).
Aetobatis narinari (non Euphrasen): Müller & Henle, 1841: 179 (India, Red Sea).
Raja edentula Forster in Lichtenstein, 1844: 227, 256 (type locality: Tanna, Vanuatu).
Stoasodon narinari (non Euphrasen): Cantor, 1849: 1416 (Penang, Malay Peninsula, Singapore).
Goniobatis meleagris Agassiz, 1858: 385 (type locality: Hawaiian Islands). Description poor and no types allocated; likely refers to this species as is only myliobatid found off Hawaii.
Myliobatis punctatus Miklukho-Maclay & Macleay, 1886: 675, pl. 4, figs 1–6 (type locality: Admiralty and Lub Islands, Australia).
Miliobatis punctatus: Miklukho-Maclay & Macleay, 1886: pl. 46 (Australia). Misspelling in original description.
Aetobates narinari (non Euphrasen): Sauvage, 1891: 519 (Madagascar).
Aetobatus narinari (non Euphrasen): Brigham, 1902: 20 (Honolulu).
Aetobatis guttata (non Bloch & Schneider): Annandale, 1909: 56 (Bay of Bengal).
Aetobatis punctatus: Günther, 1910: 497 ('south Sea')
Pteromylaeus punctatus: Garman, 1913: 439 (Admiralty Islands).
Aetobatus punctatus: Whitley, 1940: 224, figs 251, 257 (Australia).
Aetobatus flagellum (non Bloch & Schneider): Misra, 1959: 108, fig. 30 (India).
Stoasodon ocellatus: Whitley, 1964: 34 (Australia).
?Aetobatus guttatus (non Bloch & Schneider): Compagno, 1999: 497.
Aetomylaeus ocellatus: Sujatha, 2002: 157 (India).
Aetobatus cf. *narinari*: Compagno *et al*., 2005: 77 (Philippines).
?Aetobatus cf. *guttatus*: Compagno *et al*., 2005: 78 (Philippines).

Neotype. MZB 18225, juvenile male 477 mm DW (1422 mm TL), Muara Angke fish landing site, Jakarta, Indonesia, 20 May 2002.

Other material. 13 specimens: CSIRO H 2490–01, juvenile male 456 mm DW (1330 mm TL), east of Brunswick Heads, New South Wales, Australia, 29°24′ S, 153°23′ E, 25–28 m, 08 Jun. 1990; CSIRO H 4426–19, female 498 mm DW (tail removed beyond dorsal fin), Muara Angke fish landing site, Jakarta, Indonesia, 17 Oct. 1995; CSIRO H 6131–02, juvenile male 577 mm DW (1528 mm TL), Muara Angke fish landing site, Jakarta, Indonesia, 06 Apr. 2001; IPMB 38.01.07 (head only), Kota Kinabalu fish market, Sabah, Malaysia, 04 May 2004; IPMB 38.01.08, juvenile male 704 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 30 May 2003; IPPS BO296, juvenile male 447 mm DW (1309 mm TL), Mukah, Sarawak, Malaysia, 02°53.52′ N, 112°05.44′ E, 22 May 2003; IPPS HBO2, female 740 mm DW (tail damaged), Sarawak, Malaysia, 2002; MNHN A8905 (holotype of *Raja quinqueaculeata*, dried dorsal fin and stinging spines only), Guam, ~13°30′ N, ~145° E, ca. 1817–1820; RMNH 33021, juvenile male 417 mm DW, Tami River, Papua New Guinea, 24 Jun. 1955; RMNH unregistered, female 482 mm DW (1322 mm TL), Halmahera Sea, Indonesia; SMEC 75, female 371 mm DW (tail missing), SMEC 76, juvenile male 352 mm DW (tail missing), Kota Kinabalu fish landing site, Sabah, Malaysia, Oct. 1996; SMEC 244, female 481 mm DW (1362 mm TL), Kota Kinabalu fish landing site, Sabah, Malaysia, 1997.

DIAGNOSIS.— A large *Aetobatus* (reaching at least 300 cm DW) with the following combination of characters: dorsal surfaces with a dark greenish grey base coloration, variably white spotted (rarely ocellated); different NADH2 gene structure; relatively long tail (mean total length 281% DW, mean anterior cloaca to tail tip 230.2% DW); stinging spines relatively long (mean length of first spine 9.7% DW); teeth plates in a single row, those in lower jaw chevron-shaped; pectoral-fin radials about 102–116 (excluding proterygial radials anterior of eyes); total vertebral centra (including synarcual) 99–101.

DESCRIPTION.— Disc diamond-shaped, very broad but relatively short, width about 1.85 (1.63–1.80) times disc length; anterior projection 4.06 (3.54–4.27) in disc length; axis of greatest width of disc well posterior to scapular region, over abdominal cavity, its horizontal distance from snout tip 1.28 (1.16–1.43) times in distance from tip of snout to pectoral-fin insertion; deep, greatest thickness above scapular region and posterior head, thickness 7.92 (7.86–8.86) in disc width; without denticles, ridges or thorns. Pectoral fins very large, wing-like, narrowly triangular, weakly falcate; anterior margin concave basally, nearly straight for first two thirds, moderately to strongly convex distally; apex narrowly rounded to subangular, pectoral angle 56 (52–64)°; posterior margin moderately concave anteriorly, almost straight posteriorly; free rear tip broadly rounded; inner margin convex distally, becoming nearly straight anteriorly; length of anterior margin 49.8 (47.8–51.4)% DW, 1.33 (1.23–1.35) times its base length, inner margin

Figure 1. Neotype of *Aetobatus ocellatus* (MZB 18225, juvenile male 477 mm DW): A. dorsal view (fresh); B. ventral view (preserved).

Table 2. Morphometric data for the neotype of *Aetobatus ocellatus* (MZB 18225) and ranges and means of 11 other specimens, with ranges and means provided for 5 specimens of *Aetobatus narinari* from the Western Atlantic. Measurements expressed as a percentage of disc width.

	Aetobatus ocellatus				*Aetobatus narinari*		
	Neotype	Other specimens (n=11)			n=5		
		Min.	Max.	Mean	Min.	Max.	Mean
Disc width (mm)	456	352	740	502.3	420	652	532.8
Total length	298.1	264.8	292.8	281.4	229.4	277.1	263.1
Pre-dorsal length	53.8	53.5	58.6	56.5	56.2	60.2	57.8
Disc, length	54.1	55.7	61.4	58.1	56.9	62.7	59.7
Snout to pectoral-fin insertion	47.3	48.1	54.1	51.3	50.6	53.7	51.7
Disc thickness	12.6	11.3	12.7	12.2	8.6	13.3	11.3
Snout to pectoral-fin origin	13.3	13.2	16.9	15.3	14.2	17.8	16.2
Posterior orbit to pectoral-fin insertion	39.2	37.1	42.3	40.7	39.6	42.8	41.3
Snout to maximum width (horiz.)	36.9	33.7	45.5	39.3	34.8	42.3	39.2
Pectoral-fin anterior margin	49.8	47.8	51.4	49.5	48.7	50.2	49.6
Pectoral-fin posterior margin	47.3	44.4	49.3	47.7	44.8	51.2	48.0
Pectoral-fin base length	37.4	35.7	40.2	38.8	38.1	40.9	39.4
Pectoral-fin inner margin	6.1	6.0	7.3	6.8	6.2	7.7	7.1
Head length (ventral)	24.7	25.3	29.9	27.3	26.5	28.4	27.6
Preorbital length	8.0	8.3	10.3	9.3	9.1	9.9	9.5
Preorbital length (horiz.)	4.6	5.0	7.0	6.1	6.1	7.2	6.7
Head width at pectoral-fin origins	16.1	15.2	17.5	16.5	13.7	18.1	16.3
Head height at pectoral-fin origins	9.5	10.2	12.1	11.1	8.9	11.9	10.5
Head width at mid-eye	14.4	12.9	16.3	14.6	11.9	14.7	13.7
Head height at mid-eye	8.6	8.7	10.7	9.8	8.2	10.0	9.2
Interorbital width	9.2	8.4	10.4	9.5	9.4	10.6	9.9
Interspiracular width	10.5	9.2	11.1	10.3	9.3	11.1	10.2
Spiracle length (longest)	5.0	4.4	6.2	5.1	4.7	5.4	5.0
Spiracle width (narrowest)	2.0	1.7	2.8	2.3	1.6	2.3	2.0
Orbit diameter	4.7	4.0	5.6	4.8	4.1	5.5	4.6
Eye diameter	2.2	1.7	2.3	2.0	1.7	2.6	2.0
Orbit and spiracle length	11.4	9.9	12.3	10.9	9.5	11.7	10.7
Preoral length	8.6	9.6	12.3	10.5	10.7	11.3	10.9
Prenasal length	6.4	6.4	8.1	7.3	7.1	8.3	7.7
Prenasal length (horiz.)	6.1	5.7	7.6	6.6	6.7	7.6	7.2
Rostral lobe width	8.1	8.5	10.0	9.3	8.3	9.9	9.3
Rostral lobe length	3.2	2.9	5.3	4.5	4.7	6.0	5.2
Mouth width	7.8	6.8	8.1	7.4	6.4	7.7	7.2
Internarial width (external)	4.5	3.9	5.0	4.3	3.9	5.1	4.5
Nasal curtain length	4.4	4.2	5.4	4.7	3.8	5.0	4.4
Nasal curtain width	7.4	6.6	8.2	7.2	6.7	8.0	7.5
Nostril length (internal)	3.3	2.6	3.6	3.3	2.3	3.4	2.8
Width of first gill slit	1.8	1.6	2.2	1.8	1.7	2.2	1.9
Width of third gill slit	2.1	1.6	2.1	1.9	1.8	2.5	2.1
Width of fifth gill slit	1.5	1.2	1.8	1.5	1.2	1.7	1.4
Distance between first gill slits	15.7	15.4	17.8	16.1	14.5	16.6	15.7
Distance between fifth gill slits	9.6	9.6	11.4	10.2	9.3	9.8	9.5
Tail at axil of pelvic fins (width)	3.3	2.6	3.7	3.2	2.9	3.5	3.2

Table 2. cont'd.

	Aetobatus ocellatus				*Aetobatus narinari*		
	Neotype	Other specimens (n=11)			n=5		
		Min.	Max.	Mean	Min.	Max.	Mean
Tail at axil of pelvic fins (height)	3.3	2.8	4.0	3.3	3.0	3.5	3.2
Tail at origin of stinging spine(s) (width)	1.7	1.2	1.9	1.5	1.4	1.8	1.6
Tail at origin of stinging spine(s) (height)	1.9	1.3	2.1	1.9	1.5	2.5	2.1
Pectoral-fin insertion to spine origin (horiz.)	13.6	10.8	13.3	12.2	11.7	12.4	12.1
Length of first stinging spine	–	9.2	10.6	9.7	8.3	9.6	8.9
Length of second stinging spine	–	–	–	–	9.3	9.3	9.3
Pectoral-fin insertion to dorsal-fin origin (horiz.)	7.0	5.0	6.5	5.8	6.0	7.2	6.4
Dorsal-fin length	4.8	4.7	5.8	5.2	4.8	6.1	5.4
Dorsal-fin anterior margin	4.8	4.7	5.7	5.2	4.8	6.2	5.2
Dorsal-fin height	2.7	2.7	3.2	2.9	2.7	3.7	3.1
Dorsal-fin posterior margin	2.4	2.2	2.8	2.5	2.3	2.8	2.5
Dorsal-fin inner margin	1.1	0.9	1.4	1.1	0.8	1.1	1.0
Snout to anterior cloaca	47.4	48.9	55.3	51.1	50.2	53.1	51.9
Cloaca anterior to tail tip	246.8	213.7	241.1	230.2	177.1	226.9	208.3
Cloaca anterior to stinging spine	13.1	11.5	13.5	12.5	11.7	14.6	13.1
Width across pelvic fin bases	10.5	9.5	11.4	10.6	10.2	12.3	11.0
Greatest span of pelvic fins	0.0	16.3	22.5	19.8	18.9	24.2	21.9
Pelvic-fin length	12.9	13.9	16.7	15.5	14.8	17.6	15.7
Pelvic-fin anterior margin	11.8	12.2	14.2	13.4	13.1	15.1	13.8
Pelvic-fin base	6.1	6.2	8.1	7.4	5.5	7.4	6.9
Pelvic-fin posterior margin	7.1	6.3	8.7	7.5	6.3	8.9	7.6
Pelvic-fin inner margin	11.8	9.0	10.4	9.7	7.1	12.2	10.2

6.17 (4.96–6.65) in its base; origin over anterior edge of spiracles; apex located posteriorly to pectoral mid-base; insertion just posterior to pelvic-fin origin; free rear tip partly overlapping pelvic-fin anterior margin.

Head pronounced, deep, short and broad; projecting well anteriorly from pectoral-fin origins; subhexagonal in cross-section at pectoral-fin origin; cranial region of head broadly rounded in dorsoventral view; chondrocranium pronounced above eyes and spiracles; snout abruptly convex before eyes, becoming deeply concave at origin of rostral lobe; nearly straight to slightly convex ventrally; ventral head length 24.7 (25.3–29.9)% DW, 1.53 (1.57–1.76) times width at pectoral-fin origins, 5.33 (3.95–5.09) times preorbital length (horizontal), 2.69 (2.72–3.08) times interorbital width; preoral snout length 1.10 (1.20–1.76) times mouth width, 1.89 (2.03–2.93) times internarial width, 0.55 (0.59–0.73) times distance between first gill slits; head width at pectoral-fin origin 16.1 (15.2–17.5)% DW, 1.69 (1.34–1.59) times its height. Rostral lobe fleshy, moderately long (shortest in juveniles); narrowly parabolic in dorsoventral view with a narrowly rounded apex; bluntly pointed in lateral view; its length 3.2 (2.9–5.3)% DW, 7.78 (5.14–9.22) in head length, its width 1.98 (1.68–1.93) in head width at pectoral-fin origin.

Interorbital space relatively broad, convex but with a broad medial depression, without ridges, denticles or thorns; interorbital width 9.2 (8.4–10.4)% DW, 1.94 (1.80–2.35) times orbit length, 0.64 (0.58–0.71) times head width at mid-eye. Eyes moderately small, subcircular, lateral to very slightly ventrolateral on head; orbit only slightly elevated above head, diameter 2.25 (2.09–3.03) in spiracle length, 7.30 (7.18–9.36) in head width at pectoral-fin origin. Spiracles large, suboval, situated dorsolaterally posterior to orbit and above pectoral-fin origin, more visible dorsally than laterally; margins without any protuberances or folds; length 5.0 (4.4–6.2)% DW, 2.48 (1.85–2.86) times width.

Nostril narrowly suboval (often distorted after capture), immediately preceded by a broad, shallow, fleshy depression bordering anterolateral margin of the nasal curtain; anterior nasal fold thin, membranous, internal (often barely visible); very deep oronasal groove present; internarial space 1.42 (1.48–1.93) in prenasal length, 1.39 (1.16–1.49) times nostril length. Nasal curtain

large, elongate, lobate, width 1.68 (1.33–1.73) times length; lateral margin straight to concave, smooth edged; posterior margin divided by deep medial notch, bordered by a long, curtain-like fringe, not following contour of lower jaw; posterior margin of each lobe convex with apices narrowly rounded; most of surface finely papillate, covered with minute pores; apex and posterolateral margin recessible within oronasal groove.

Mouth moderately large, transverse, located ventrally, width 7.8 (6.8–8.1)% DW, 0.91 (0.57–0.83) times preoral length, 2.07 (2.05–2.50) in head width at pectoral-fin origin; not protrusible, anterior teeth of lower jaw visible when mouth closed; buccal region intricately papillate; skin on chin and at margin of lower jaw fleshy, strongly furrowed, papillate, indented slightly at symphysis. Teeth in a single row in each jaw, coalesced to form plates; about 9 narrow, lingually recurved teeth in upper jaw (Fig. 5a), tooth plate well inside palate, its length about half its width; about 18 narrow, chevron-shaped teeth in lower jaw (Fig. 5b), tooth plate protruding distally, its length more than twice its width; roof of mouth with 2 rows of oral papillae, 4 in outer row, 7 in inner row, those in outer row slightly larger than those of inner row; floor of mouth near lingual margin of lower tooth plate with lunate fringe of about 7 variably shaped (usually pointed), less regular oral papillae.

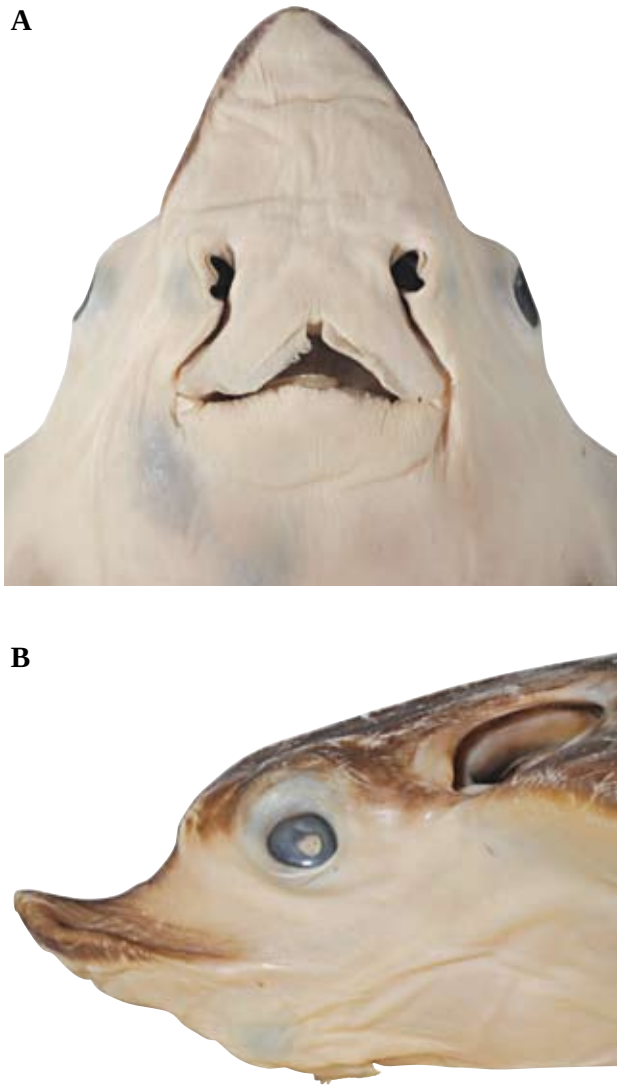

Figure 2. *Aetobatus ocellatus* (CSIRO H 6131–02, juvenile male 577 mm DW, preserved): A. ventral head view; B. lateral head view.

Gill openings small, elongated S-shaped, forming a weakly fringed lobe laterally; length of first gill slit 1.20 (1.10–1.41) times length of fifth gill slit, 4.3 (3.18–5.06) in mouth width; distance between first gill slits 3.45 (3.20–4.23) times internarial space, 0.64 (0.55–0.61) times ventral head length; distance between fifth gill slits 2.12 (2.01–2.70) times internarial distance, 0.39 (0.35–0.41) times ventral head length.

Pelvic fins relatively large, slender, subquadrangular, anterior margin concave, apex broadly angular, posterior margin strongly convex, free rear tip broadly rounded, inner margin weakly convex; extending well beyond pectoral-fin free tips; pelvic-fin length 12.9 (13.9–16.7)% DW, 1.24 (1.33–1.61) times width across fin bases, inner margin 11.8 (9.0–10.4)% DW. Claspers of adult males not examined in detail.

Dorsal fin small, strongly raked, its origin posterior to pelvic-fin insertions by about half of its fin base; anterior margin weakly convex; apex broadly rounded, over insertion of fin; posterior margin slightly convex to straight; free rear tip angular, inner margin very short, nearly straight; predorsal length 1.86 (1.71–1.87) in disc width, fin length 4.8 (4.7–5.8)% DW, height 0.57 (0.51–0.64) times its length, inner margin 4.33 (3.57–5.83) in fin length.

Tail very long, slender, whip-like, its length (from cloaca origin) 2.47 (2.14–2.41) times disc width; tapering gradually at base to stinging spine, and gradually becoming more whip-like beyond sting; base moderately compressed, suboval in cross section at pelvic-fin insertion, tail width at pelvic insertion 1.00 (0.89–1.09) times height; rhomboidal in cross section near origin of stinging spine, width 0.89 (0.62–0.95) times height at first spine origin; no skin folds present; a weak naked groove on dorsal surface of tail immediately posterior to base of stinging-spine(s), almost fully housing spines. Stinging spines 0–5, second longest (when more than one present), very elongate, slender, moderately broad-based, strongly tapered, almost fully serrated laterally; distance from sting base to pectoral-fin insertion 13.6 (10.8–13.3)% DW; longest stinging spine (9.2–10.6)% DW, (1.58–2.15) times dorsal-fin length.

Vertebral centra total (including synarcual) 101 (99–100, n=3); total (excluding synarcual) 97 (94–96);

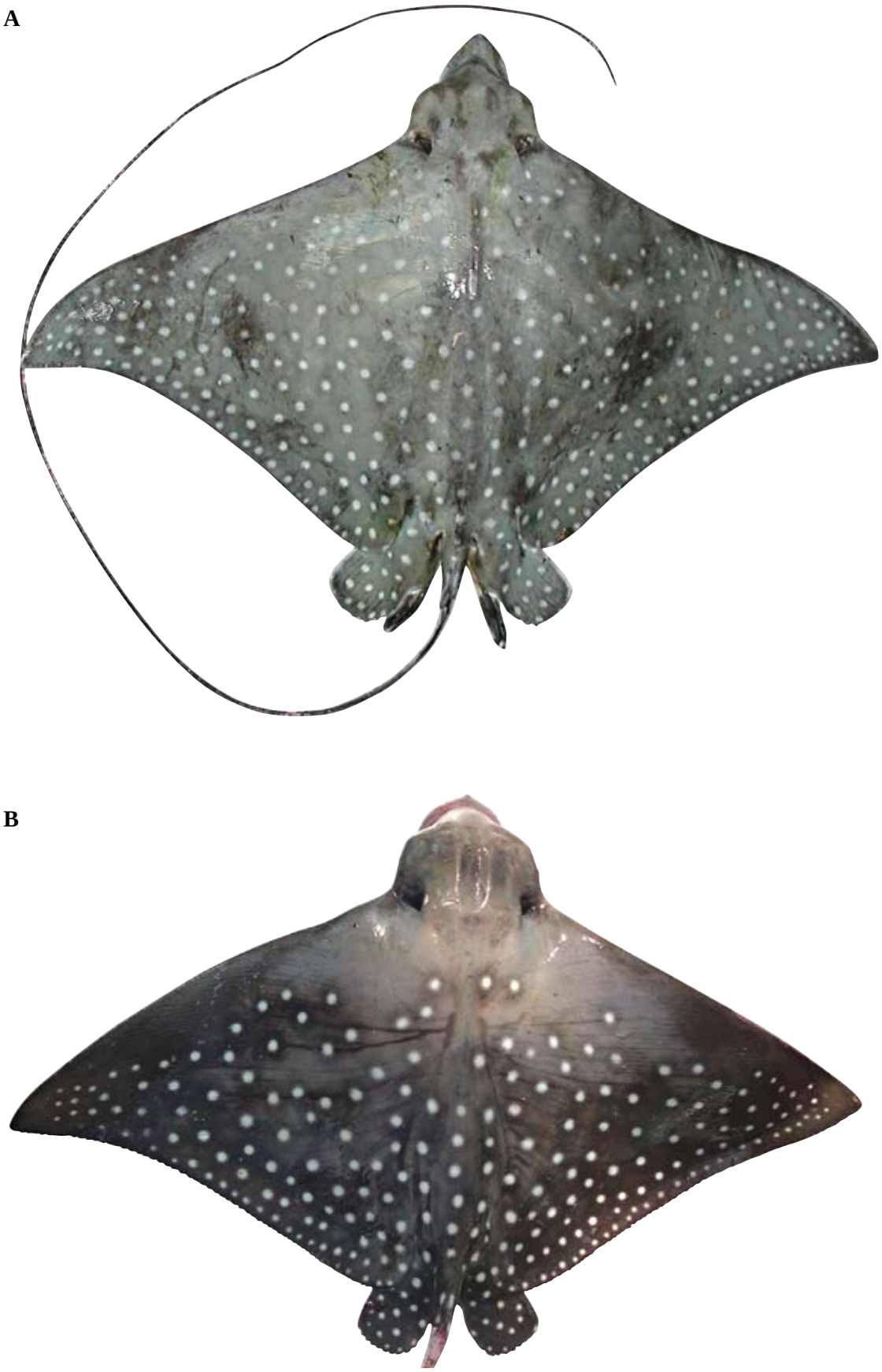

Figure 3. Dorsal view of *Aetobatus ocellatus*: A. not retained (field number BOD52, Sandakan, Sabah), adult male 1260 mm DW (fresh); B. IPPS BO296, juvenile male 465 mm DW (fresh).

Figure 4. Lateral tail of *Aetobatus ocellatus*: A. CSIRO H 2490–01, juvenile male 456 mm DW; B. MNHN A8905 (holotype of *Raja quinqueaculeata*, dried dorsal fin and stinging spines only).

monospondylous (including synarcual) 45 (41–45); monospondylous (excluding synarcual) 41 (36–41); pre-dorsal diplospondylous 26 (25–31); post-sting diplospondylous 30 (27–33). Total pectoral-fin radials (excluding propterygial radials anterior of eyes) 102*–107 (109*–116); propterygium (anterior of eyes) ? (11*–16*), propterygium (posterior of eyes) 11* (12*–14), mesopterygium 36–37 (32–37), metapterygium 55*–59* (62*–66). Pelvic-fin radials: 1, 4* (1, 4*–6) + 15* (14*–16).

COLOUR.— When fresh, based on neotype: Dorsal surface greenish grey, slightly darker along posterior margins of pectoral and pelvic fins; all of disc and pelvic fin, and parts of raised portion of head, covered with large, diffuse-edged white spots; spots reasonably similar in size (slightly smaller near disc margin) and evenly spaced; eye bluish black; dark (dorsal) and pale (ventral) surfaces well demarcated (waterline) at anterior edge of disc and its junction with head; waterline extending anteriorly to mid eye and onto forehead; dark dorsal surface on rostral lobe similar, contrasted with its paler ventral surface and posteriorly with pale mid-snout; tail uniform greyish green. Ventral surface yellowish white; edge of rostral lobe dark in some material; outer anterior margin of disc black. Other material: Base colour of dorsal disc variable, greenish, greyish or reddish brown; coverage of white spots variable, usually densest posteriorly, but sometimes confined to posterior edge of disc or absent; dorsal fin and clasper of adult male plain coloured, similar to pelvic fin.

SIZE.— The 12 measured specimens examined ranged from 352–740 mm DW (1309–1528 mm TL, n=6) and consisted entirely of immature individuals. Since this species was previously considered as a synonym of *A. narinari*, accurate size information relating to *A. ocellatus* is difficult to separate from data for other species of the *A. narinari* complex. Last & Stevens (2009) report that in Australia, this species (as *A. narinari*) attains up to 3000 mm DW (>8800 mm TL), with males and females maturing at 1000 and 2140 mm DW respectively, and born at 180–260 mm DW. White & Dharmadi (2007) recorded a maximum size of 2144 mm DW for females and 1544 mm DW for males, with 50% male maturity at 998 mm DW. Other specimens recorded during recent surveys of Borneo ranged in size from 510–960 and 640–1320 mm DW for females (3) and males (6) respectively.

DISTRIBUTION.— *Aetobatus ocellatus* is probably widely distributed throughout the tropical and subtropical Indo–West and Central Pacific. Specimens examined in this study were from Australia, Indonesia, Borneo and Guam. The Indo–West and Central Pacific clade in Richards *et al.* (2009) included specimens from Japan, China, Hong Kong, Indonesia and Hawaii. This species is also likely to be present in the Western Indian Ocean, but specimens in collections from this area are generally lacking.

METAZOAN PARASITES.— *Aetobatus laticeps*:

Published records of metazoan parasites likely to have come from individuals of *A. laticeps* are limited. They consist of only 2 species of tapeworms; both are species of the onchobothriid genus *Acanthobothrium* reported from the spiral intestines of their hosts. These are *Acanthobothrium nicoyaense* described by Brooks & McCorquodale (1995) from the Gulf of Nicoya, western coast of Costa Rica and *Acanthobothrium monksi* described by Marques *et al*. (1997) from the coast of Ecuador.

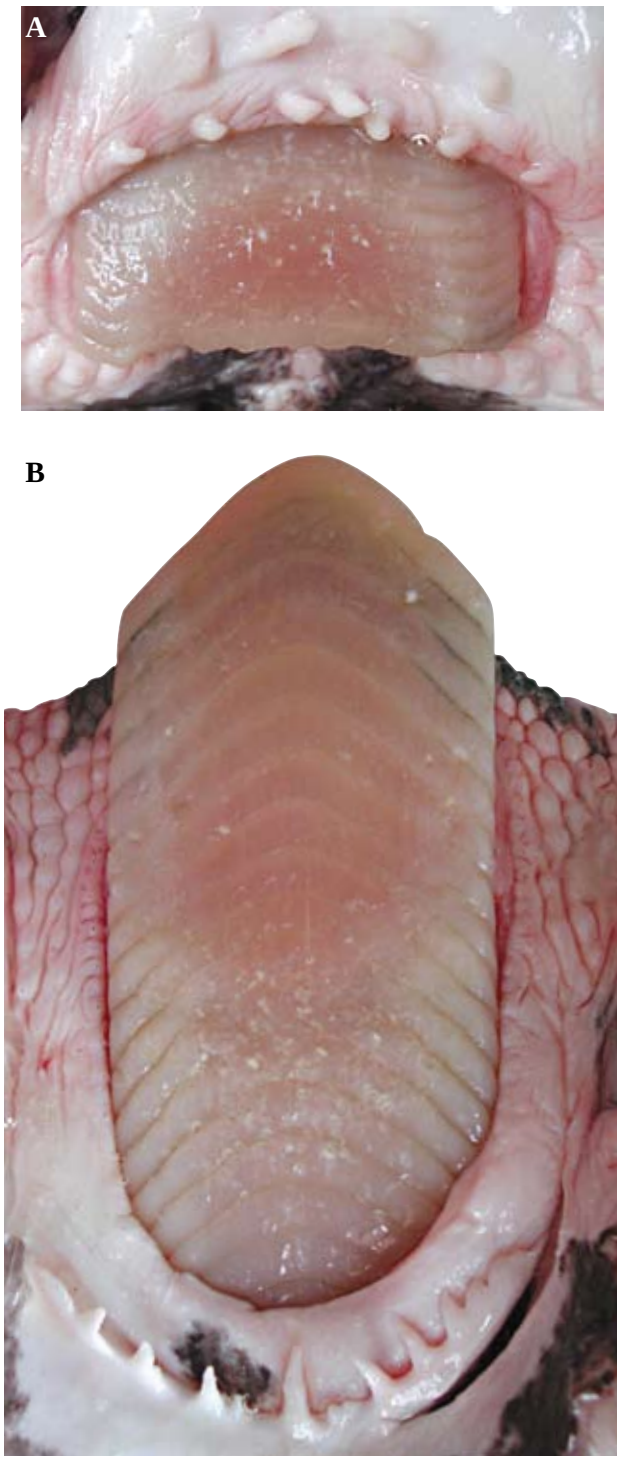

Figure 5. Tooth plates and oral papillae of *Aetobatus ocellatus* (specimen dissected, not retained, from Sabah, Malaysia): A. upper jaw; B. lower jaw.

***Aetobatus narinari* sensu stricto:** A slightly more diverse suite of metazoan parasites has been reported from spotted eagle rays from the Eastern Atlantic; records from the Western Atlantic are lacking altogether. These parasites consist of the leeches *Branchellion torpedinis* reported from spotted eagle rays from Venezuela by Pauls & Provenzano (1999) and *B. ravenelii* from spotted eagle rays, presumably from the northern Gulf of Mexico (Sawyer *et al*., 1975). Two species of monocotylid monogeneans have also been reported. *Decacotyle floridana* was reported from spotted eagle rays in Beaufort, North Carolina by Pearse (1949) (as *Heterocotyle floridana*), by Hargis (1955a) (as *Heterocotyle aetobatis*), from the Gulf of Mexico off Florida, and from the Yucatán Peninsula in Mexico by Lamothe-Argumedo *et al*. (1997) (also as *H. aetobatis*) and Pulido-Flores & Monks (2005). In addition, *Thaumatocotyle pseudodasybatis* was described by Hargis (1955b) from the ventral surface of spotted eagle rays from the Gulf of Mexico, Florida. In addition, 4 species of tapeworms have been reported from the spiral intestines of spotted eagle rays taken from localities in the Western Atlantic. The lecanicephalidean *Tylocephalum marsupium* and the tetraphyllidean *Acanthobothrium tortum* (as *Onchobothrium tortum*) were described by Linton (1916) from the Dry Tortuga Islands off Florida, and *A. tortum* was later also reported from Venezuela (Mayes & Brooks, 1981). A second species of *Acanthobothrium*, *A. colombianum* was described by Brooks & Mayes (1980) from the Caribbean Sea off Colombia. Furthermore, Mayes & Brooks (1981) reported *Disculiceps* sp. from the spotted eagle ray in Venezuela. Given that this genus normally parasitises carcharhiniform sharks, the latter specimens seem likely to represent *Tylocephalum*, a lecanicephalidean genus which, like *Disculiceps*, possesses a globose scolex, but which, unlike *Disculiceps*, commonly occurs in other myliobatiform rays.

Aetobatus ocellatus: By far the greatest diversity of metazoan parasites of spotted eagle rays have come from those collected in localities throughout the Pacific and Indian Oceans. Records include gnathid isopods (*Gnathia nublia*) described from the gills from spotted eagle rays from Japan (Ota & Hirose, 2009). Four species of nematodes have been reported from the digestive system. These consist of the anisakid *Hysterothylacium aetobatum* described by Lakshmi (2005) from India, and 3 species of gnathostomid nematodes of the genus *Echinocephalus*, specifically *Echinocephalus sinensis* from Australia and New Caledonia (see Beveridge, 1987 and Moravec & Justine, 2006 respectively), and *Echinocephalus spinosissimus* and *E. uncinatus* both from India by Shafee & Natarajan (1976). A total of 7 species of monocotylid monogeneans have been

reported from the gill and nasal tissue, and dorsal skin of spotted eagle rays. These include the 2 species treated above reported from *A. narinari* sensu stricto from the Atlantic Ocean, specifically *Decacotyle floridana* which has been reported from Hawaii by Yamaguti (1968) [as *Alloheterocotyla* (*Heterocotyle*) *aetobatis*] and from Heron Island, Australia by Chisholm & Whittington (1998), and *Thaumatocotyle pseudodasybatis*, reported from New Caledonia and French Polynesia by Marie & Justine (2005, 2006). The following 5 species of monocotylid monogeneans are known only from Indo-Pacific localities (see Marie & Justine, 2006): *Clemacotyle australis, Decacotyle elpora, Decacotyle octona, Dendromonocotyle torosa* and *Empruthotrema kearni*.

However, tapeworms represent the most diverse elements of the metazoan fauna of Pacific and Indian Ocean spotted eagle rays. Records to date include a total of 28 species representing 4 orders of tapeworms; all species parasitize the digestive system of their hosts, with most occupying the spiral intestine of their hosts. The single diphyllidean, *Echinobothrium boisii*, was reported from Sri Lanka by Southwell (1911). Five species of tetraphyllideans including 3 species of *Acanthobothrium*, have also been reported. These are *A. aetiobatis* reported by Shipley (1900) from Lifu in the Loyalty Islands, *A. dysbiotos* reported by MacCallum (1921) from Jakarta (as Batavia), Java, Indonesia, and *A. arlenae* described by Campbell & Beveridge (2002) from northern Australia. The remaining 2 tetraphyllideans are the only described species in their respective genera: *Myzocephalus narinari* and *Myzophyllobothrium rubrum*. These were both reported by Shipley & Hornell (1906) from the Gulf of Mannar between India and Sri Lanka. Eight species of trypanorhynchs, each representing a different genus, have also been reported. These include 4 species of the family Eutetrarhynchidae: *Didymorhynchus southwelli* from Sri Lanka (see Beveridge & Campbell, 1988), *Dollfusiella aetobati* from northern Australia (see Beveridge, 1990), *Oncomegas australiensis* also from northern Australia (see Toth *et al*., 1992) and *Parachristianella baverstocki* from India (see Palm, 2004). In addition, the tentaculariid *Kotorella pronosoma* has been reported from Java by MacCallum (1917), the otobothriid *Proemotobothrium linstowi* was reported by Palm (2004) from Singapore, the rhinoptericolid *Shirleyrhynchus aetobatidis* was originally described from Sri Lanka by Shipley & Hornell (1906), and the mixodigmatid *Trygonicola macroporus* was reported from spotted eagle rays from Malaysia by Beveridge & Campbell (1998).

In total, 14 species of lecanicephalidean tapeworms have been reported from spotted eagle rays in the Pacific and Indian oceans. Unfortunately, many of these are known only from their somewhat brief original descriptions which appeared early in the 20th C and are among the earliest reports of parasites from spotted eagle rays ever published. For example, Shipley (1900) described *Adelobothrium aetiobatidis* from Lifu in the Loyalty Islands. Shortly thereafter, Shipley & Hornell (1905) described *Staurobothrium aetobatidis* and *Tylocephalum aetiobatidis* (originally as *Tetragonocephalum aetiobatidis*) and Shipley & Hornell (1906) described *Cephalobothrium aetobatidis*, *Hornellobothrium cobraformis* and *Kystocephalus translucens*, all 5 of the latter species from eagle rays collected from the Gulf of Mannar between Sri Lanka and India. A few years later, Southwell (1911) described *Calycobothrium typicum* (as *Cyclobothrium typicum*) from Sri Lanka, MacCallum (1917) described *Tenia narinari* presumably from Jakarta (as Batavia), Java, Indonesia and Southwell (1925) described *Tylocephalum yorkei* from India. More recently, new reports have come from Australia. For example, Butler (1987) reported *Hornellobothrium cobraformis* from Moreton Bay, Australia. However, Jensen (2005) considered the 2 specimens deposited by Butler, to represent 2 species distinct from *H. cobraformis* and gave them the letter designations A and B. Jensen (2005) also described *Hornellobothrium extensivum* from northern Australia. Newer reports have come from India, for example, Jadhav & Shinde (1987) described *Tylocephalum aurangabadensis* and most recently, Pramanik & Manna (2007) described *Tylocephalum girindrai*.

However, it is important to note that the unusually large number of species of tapeworms reported from spotted eagle rays in the Pacific and Indian Oceans is cause for some concern. As noted above, the identities of the hosts of these species are based solely on geographic distribution. It would seem prudent to pay particular attention to spotted eagle rays collected from Pacific and Indian Ocean localities for these results lead us to suspect that more than the single species "*Aetobatus ocellatus*" may occur in these regions. We note that, while their results remain to be confirmed, Jensen & Caira (1998) reported differences in the lecanicephalidean tapeworm faunas of eagle rays collected from Thailand and Australia. If it is ultimately determined to be the case that more than a single species of spotted eagle ray occurs in the Indo–Pacific, the host records described above would need further revision.

Host specificity: Comparison of the parasite records presented above for *Aetobatus laticeps*, *A. narinari* and *A. ocellatus* reveals little overlap among the metazoan parasite faunas of these host species. In fact, only 2 of the 49 taxa treated above have been reported from two of these species of eagle rays. While on the surface, this result might be interpreted to provide compelling support of the contention that these hosts do, in fact, represent distinct species, it is important to note that almost none of these parasite data were collected in a comparative framework with the explicit intent of exploring similarities and differences among the parasite faunas of these host species. In fact, to our knowledge only two studies have be undertaken with that objective in mind and the results of these studies are somewhat inconsistent. While Jensen & Caira (1998) reported differences among the faunas

of spotted eagle rays from the Eastern Pacific, Thailand and Australia, Marie & Justine (2006) found that 2 of the 7 monogenean species investigated parasitised eagle rays from both Atlantic and Pacific Ocean localities. This question would obviously benefit greatly from much more detailed and thorough investigation.

In addition, none of the studies cited above focused on documenting the full complement of metazoan parasites of spotted eagle rays from any of the target regions. Most focused on a particular component of the metazoan parasite fauna, for example monogeneans or nematodes or tapeworms, some concentrated only on subset of the latter faunas (e.g. tetraphyllidean tapeworms, lecanicephalidan tapeworms, trypanorhynch tapeworms, etc.). Investigation of the full complement of metazoan parasites of spotted eagle rays, from any locality, is also clearly in order. The metazoan parasite fauna of *Aetobatus laticeps* appears to be particularly poorly known.

DISCUSSION

As detailed in the introduction of this paper, the nomenclature of the *Aetobatus narinari* complex is very complicated, particularly in the Indo–West Pacific. This paper investigates the nomenclature of the Indo–West Pacific species in this complex and provides a redescription for this species, *Aetobatus ocellatus* (Kuhl, 1823). Since there is no type material for this species, a neotype (MZB 18225) was selected for *A. ocellatus*, which was collected during recent surveys of Indonesian fish landing sites from Java, the type locality for this species. *Aetobatus ocellatus*, which replaces *A. narinari* as the valid name for this species in the Indo–West Pacific, was compared with specimens of *Aetobatus narinari* from the Western Atlantic (see Figs 6, 7 and 8), including the locations given as the type localities for this species, i.e. Saint Barthelemy (West Indies) and Brazil.

Five significant groupings are evident in all three types of analyses (Fig. 6): (i) sequences from the Western North Atlantic form a distinct clade; (ii) sequences from specimens captured in the Gulf of California are distinct; (iii) sequences from the Western North Atlantic and the Eastern Pacific are more closely related to each other than they are to sequences from the Persian Gulf, Mozambique, South East Asia and Australia; (iv) the two specimens from Qatar form a distinct group; (v) sequences from specimens collected in the Philippines, Taiwan, Indonesia, Malaysia, Singapore and northern Australia are similar and do not exhibit compelling geographic substructure.

A major revision of the *Aetobatus narinari* complex is needed to determine its composition and the geographic ranges of its species. Results from molecular work on this complex by Richards *et al.* (2009), and those given in this study, indicate that the Eastern Pacific clade is distinct from the Western Atlantic and Indo–West/Central Pacific clades. If this clade represents a species-level separation, *Aetobatus laticeps* (Gill, 1865) described from California on the Pacific US coast would become the valid name for this species. Material from the Eastern Pacific needs to be critically compared with other members of this complex from the other ocean basins. Material from the Eastern Atlantic is unusually sparse and thus little information is available for this region currently. Richards *et al.* (2009) proposed an Indo–West Pacific origin for the *A. narinari* species complex with a westerly dispersal into the Atlantic from around the southern tip of Africa and then into the Eastern Pacific. Since a barrier to dispersal has existed for a long period of time for tropical and subtropical species around the southern tip of Africa, it is very unlikely that the Eastern Atlantic species would be conspecific with *A. ocellatus* from the Indo–West Pacific. However, specimens from the Eastern Atlantic need to be critically compared to *A. narinari* from the Western Atlantic to determine whether they are conspecific. If further investigation shows that the Eastern Atlantic form is a separate species, *Aetobatus latirostris* (Duméril, 1861), described from the Gabon coast, would become the valid name for this species.

As mentioned previously, the nomenclature of *A. ocellatus* is quite complicated and a large number of synonyms (at least 29) exist for this species. Fowler (1941) summarised many of these synonyms, but two of these are not conspecific with this species. For example, Fowler (1941) lists *Dicerobatis eregoodoo* (not Cantor) from Saville-Kent (1893) as a synonym of *A. ocellatus*, but the image given in this book (Plate XLVIII) is clearly of a species of *Mobula*. Similarly, he lists *Myliobatis aquila* (not Linnaeus) as a synonym from the same source, but in Saville-Kent (1893) the name used is *Myliobatis australis*. Furthermore, the description by Kent of this species includes 'Large blue-spotted sting-rays, *Myliobatis australis*, bask lazily in the intervening sandy patches' indicating it is most likely referring to the Bluespotted Fantail Ray *Taeniura lymma*, which is particularly abundant in this area.

The comparison of *Aetobatus ocellatus* with *A. narinari* from the Western Atlantic revealed that they are very similar morphologically. There are several minor differences in morphometrics between the species, but the ranges for these overlapped: slightly longer tail in *A. ocellatus* than in *A. narinari* (mean total length 281 vs. 263% DW, mean anterior cloaca to tail tip 230.2 vs. 208.3% DW), and a longer stinging spine (mean length 9.7 vs. 8.9% DW). The major difference between these species is the background coloration of the dorsal surfaces. *Aetobatus ocellatus* has a dark greenish, greyish to almost blackish (sometimes with a pinkish tinge) background colour, whereas all Western Atlantic specimens of *A. narinari* have a much paler, medium yellowish brownish (fawn) background colour (Figs 7 and 8).

A

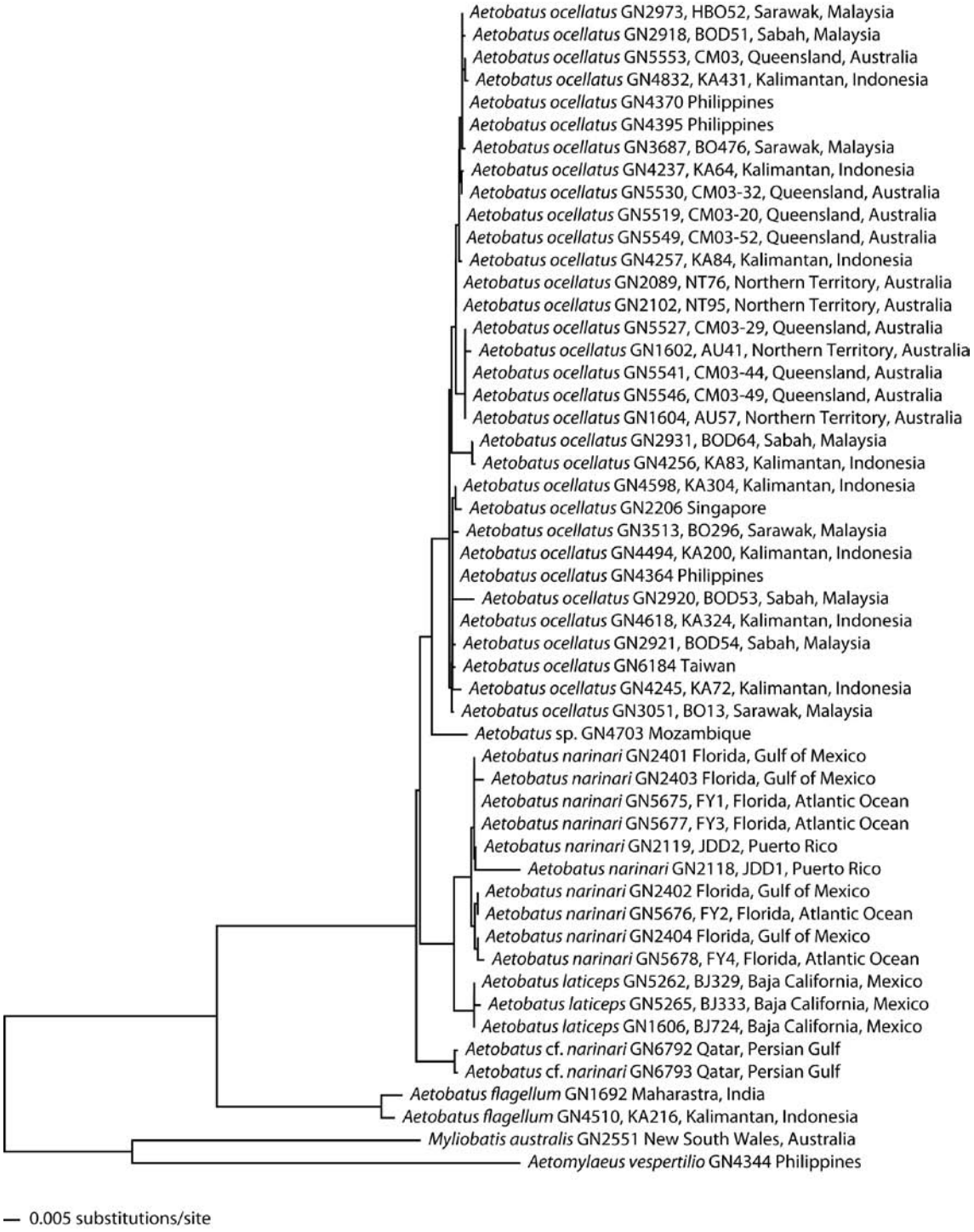

Figure 6. A. Neighbour-Joining tree based on K2P distance; B. Parsimony Bootstrap with 1000 replicates; and C. Maximum Likelihood tree using a GTR+I+Γmodel (General Time Reversible + Invariant sites + gamma distributed rates). Model parameter values were optimized recursively for the Likelihood analysis as the search progressed.

B

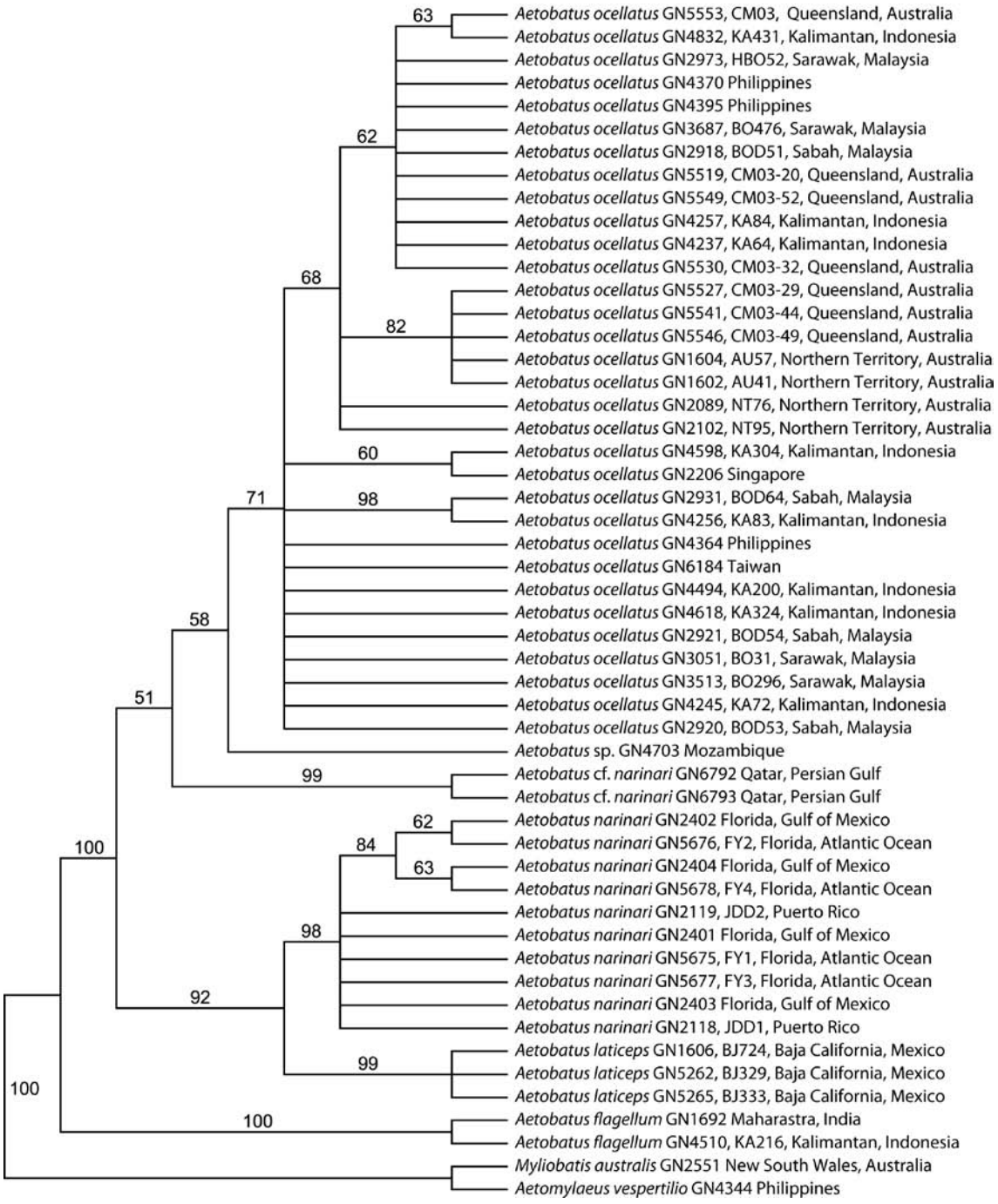

Figure 6. cont'd.

C

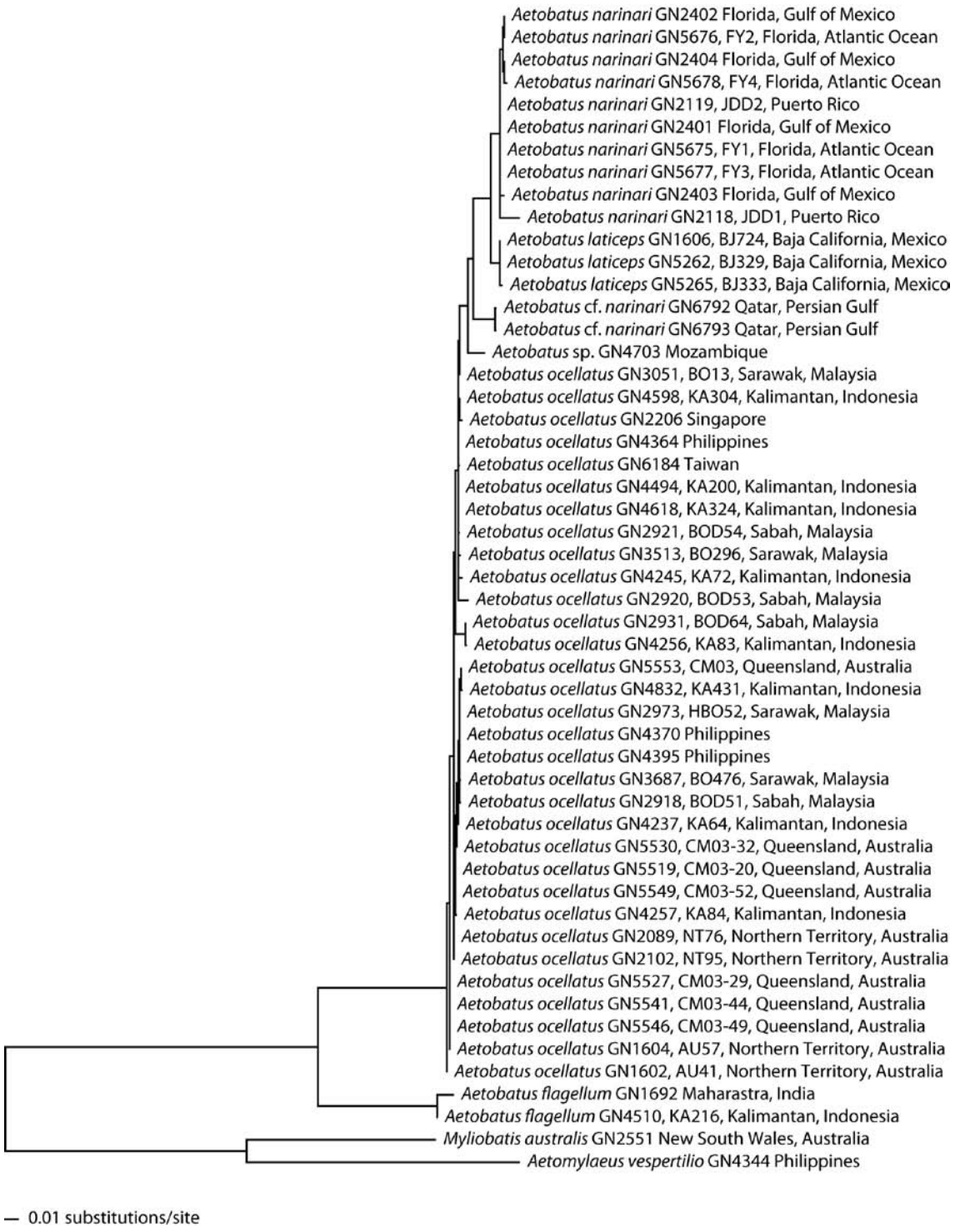

Figure 6. cont'd.

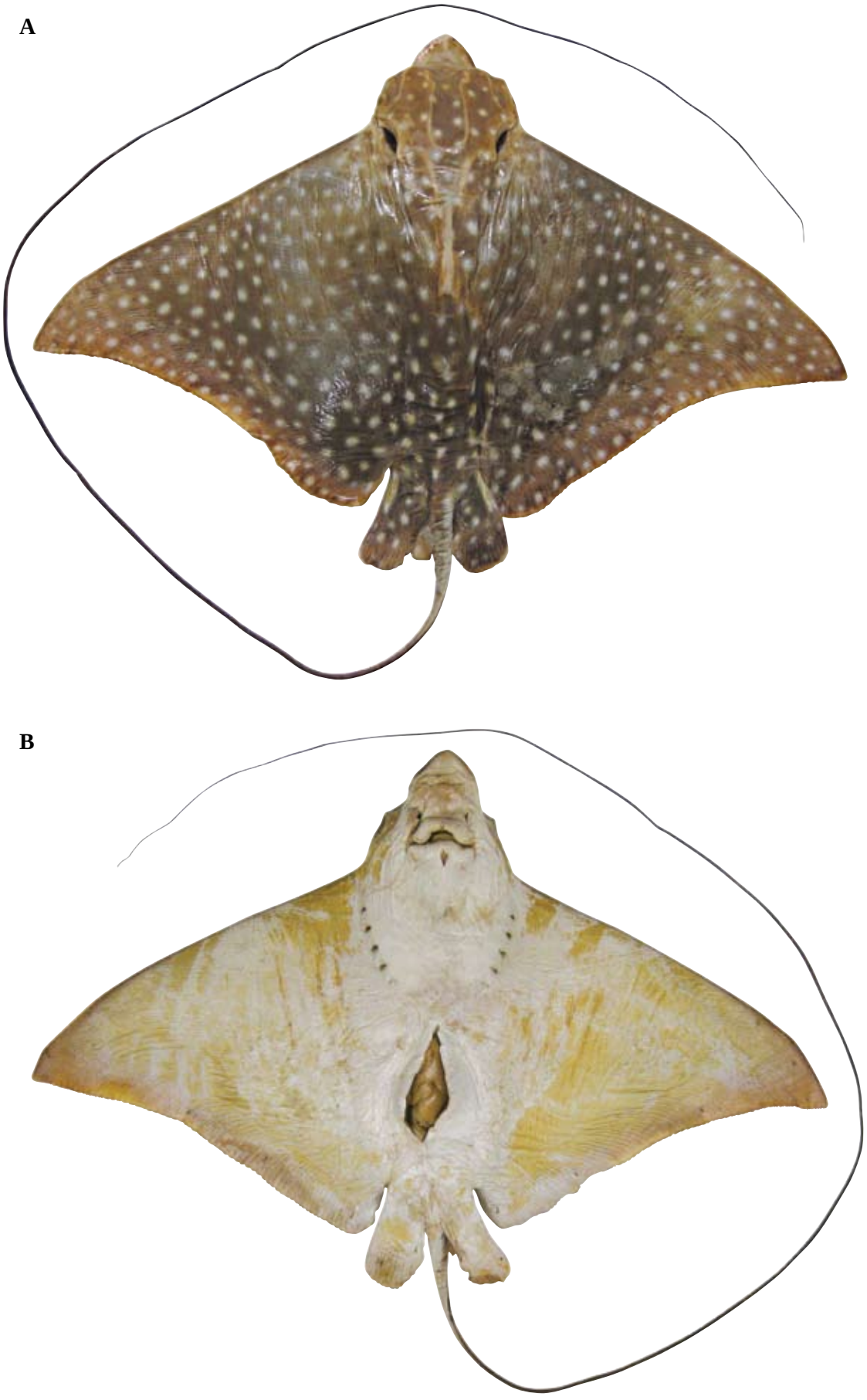

Figure 7. *Aetobatus narinari* (MNHN A7948, female 420 mm DW, preserved): A. dorsal view; B. ventral view.

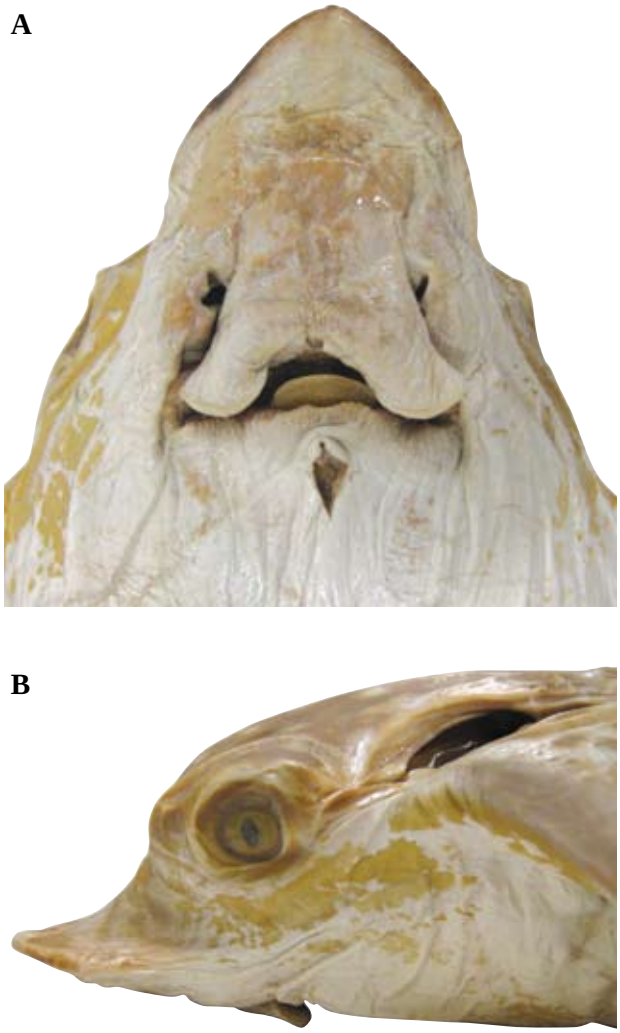

Figure 8. *Aetobatus narinari* (MNHN A7948, female 420 mm DW, preserved): A. ventral head view; B. lateral head view.

Aetobatus narinari has been assessed as Near Threatened by the IUCN Red List of Threatened Animals (Kyne *et al*., 2006), but this assessment considers it to be circumglobal; although it states that it is likely to belong to a species complex. Many of the threats listed in this assessment refer to areas in the Indo–West Pacific, thus *A. ocellatus* is probably more threatened than the other members of the complex. Based on the results of this paper and future revisions of the group, the conservation status of the species within this complex needs to be re-assessed.

Comparative material

Aetobatus narinari: 5 specimens. (Western Atlantic) BMNH 74.10.31.11, female 652 mm DW (1496 mm TL), Bermuda, North Atlantic; MNHN A7948, female 420 mm DW (1150 mm TL), Haiti, The Antilles, ca. 19° N, 73° W; MNHN A4053, juvenile male 600 mm DW (1632 mm TL), eastern Brazil, ~10° N, ~30° W; MNHN A7940 (2 juvenile males), 445 mm DW (1233 mm DW), 547 mm DW (tail tip damaged), Saint Barthelemy, French West Indies, 17°50′ N, 62°49′ W.

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Appendix 1

Morphometric measurement abbreviations and terminology used for carcharhinid sharks.

TL – Total length
PRC – Precaudal length
PD2 – Pre-second dorsal length
PD1 – Pre-first dorsal length
HDL – Head length
PG1 – Prebranchial length
POB – Preorbital length
POB (horiz) – Preorbital length (horizontal)
POR – Preoral length
PRN – Prenarial length
PRN (horiz) – Prenarial length (horizontal)
PP1 – Prepectoral length
PP2 – Prepelvic length
SVL – Pre-vent length
PAL – Preanal fin length
IDS – Interdorsal space
DCS – Dorsal-caudal space
PPS – Pectoral-pelvic space
PAS – Pectoral-anal space
ACS – Anal-caudal space
EYL – Eye length
EYH – Eye height
INO – Interorbital space
NOW – Nostril width
INW – Internarial space
ANF – Anterior nasal flap length
MOL – Mouth length
MOW – Mouth width
ULA – Upper labial furrow length
LLA – Lower labial furrow length
GS1 – First gill-slit height
GS2 – Second gill-slit height
GS3 – Third gill-slit height
GS4 – Fourth gill-slit height
GS5 – Fifth gill-slit height
HDH – Head height
TRH – Trunk height
TAH – Tail height
CPH – Caudal peduncle height
HDW – Head width
TRW – Trunk width
TAW – Tail width
CPW – Caudal peduncle width
P1L – Pectoral length
P1A – Pectoral anterior margin
P1B – Pectoral base length
P1B – Pectoral height
P1I – Pectoral inner margin
P1P – Pectoral posterior margin
P2L – Pelvic length
P2A – Pelvic anterior margin
P2B – Pelvic base length
P2H – Pelvic height
P2I – Pelvic inner margin
P2P – Pelvic posterior margin
CLO – Clasper outer length
CLI – Clasper inner length
CLB – Clasper base width
D1L – First dorsal length
D1A – First dorsal anterior margin
D1B – First dorsal base length
D1H – First dorsal height
D1I – First dorsal inner margin
D1P – First dorsal posterior margin
D2L – Second dorsal length
D2A – Second dorsal anterior margin
D2B – Second dorsal base length
D2H – Second dorsal height
D2I – Second dorsal inner margin
D2P – Second dorsal posterior margin
ANL – Anal length
ANA – Anal anterior margin
ANB – Anal base length
ANH – Anal height
ANI – Anal inner margin
ANP – Anal posterior margin
CDM – Dorsal caudal margin
CPV – Preventral caudal margin
CPL – Lower postventral caudal margin
CPU – Upper postventral caudal margin
CFW – Caudal-fin fork width
CFL – Caudal-fin fork length
CST – Caudal-fin subterminal margin
CTR – Caudal-fin terminal margin
CTL – Caudal-fin terminal lobe length
DAO – Second dorsal origin to anal-fin origin
DAI – Second dorsal insertion to anal-fin insertion
DPI – First dorsal midpoint to pectoral insertion
DPO – First dorsal midpoint to pelvic origin
PDI – Pelvic midpoint to first dorsal insertion
PDO – Pelvic midpoint to second dorsal origin

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